SPIXIANA	Supplement 20	61-98	München, 01.03.1994	ISSN 0177-7424	ISBN 3-923871-78-3

The adult males of *Parachironomus* Lenz, 1921, from the Neotropical faunal region

(Insecta, Diptera, Chironomidae)

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Spies, M., Fittkau, E. J. & F. Reiss (1994): The adult males of *Parachironomus* Lenz, 1921, from the Neotropical faunal region (Insecta, Diptera, Chironomidae). – Spixiana Suppl. **20:** 61-98

The first regional diagnosis of *Parachironomus* outside of the Holarctis is derived from Neotropical adult males, extending previous definitions of the genus. 18 species are keyed, and 17 described in detail, 14 of which are new: *aberrans, apalai, atroari, camajura, cayapo, guarani, manaos, matapi, mirim, osa, ticuna, tirio, waika,* and *yanomani.* 7 species are briefly diagnosed in the pupal stage, and compared to Holarctic species groups. *Parachironomus supparilis* (Edwards), comb. nov. is regarded a superspecies including *Parachironomus longistilus* syn. nov. and three other variant forms. Its distribution bridges the usual gap between Andean/Patagonian and Guayanan/Brazilian subfaunas. *Parachironomus puberulus* (Edwards) comb. nov. is presented. Within the Neotropical region, only three species pairs, no larger groups are identified. Biogeographic affinities are strongest to the Nearctic. *P. carinatus* (Townes) and *P. directus* (Dendy & Sublette) are the closest relatives outside of the Neotropics.

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Introduction

For a long time, systematic studies on South American Chironomidae remained limited to the Andean/Patagonian faunal subregion (e.g. Edwards 1931, Brundin 1966, Reiss 1972). In contrast to the roughly 250 forms discovered there, the number of Chironomid species for tropical South America has been estimated at around 1500 (Fittkau & Reiss 1979), of which little more than a third have been identified, much less validated.

Tab. 1 illustrates the extent, to which *Parachironomus* Lenz represents the status of knowledge on Neotropical Chironomid systematics. Since Hunter's (1900) conspectus, only 5 species have been described, which can be placed in the genus (Edwards 1931; Paggi 1977, 1979). All of these had been collected only in southern, temperate latitudes.

Lenz (1921: 160) established *Parachironomus* on the basis of larval and pupal characters. The first brief diagnosis for ♂♂ imagines was given by Edwards (1929: 338), who placed them as "series 3" in "group E *(Cryptochironomus)*" of *Chironomus (Chironomus)*, but did not include all forms known by then, which are now considered *Parachironomus*. Townes (1945) listed the Nearctic species as belonging to *Harnischia (Harnischia)*.

After several previous attempts remain invalid for various reasons, Beck & Beck (1969: 283) by subsequent designation establish *Chironomus cryptotomus* Kieffer as the type species of *Parachironomus*. Their treatment of species found in Florida includes larval and pupal descriptions. A revision of European male imagines is given by Lehmann (1970).

The three volumes on the Chironomidae of the Holarctis (Wiederholm 1983-1989) introduce comprehensive diagnoses of larvae, pupae, and ♂♂ imagines of the genus for a major faunal region (Pinder & Reiss 1983, 1986; Cranston et al. 1989). The work reported here presents the first summary of *Parachironomus* characters for a continent outside of the Holarctis.

P. robustus Paggi (1979: 50) is included in the key, but not in diagnoses for the genus and species, due to a number of strongly deviating features (for details see "Discussion").

Methods and Morphology

Except where otherwise explained, new species names were chosen to commemorate native Indian cultures of the Amazon region.

To facilitate quick comparisons, values for the standard characters of each species are compiled in table 3. The species descriptions are mostly limited to data not listed in tables, but also repeat those warranting special mention.

Morphological nomenclature follows, as far as possible, Saether (1980) and Oliver & Dillon (in Wiederholm 1989). The following further approaches are noteworthy:

Head. The width of the dorsomedial eye extensions was first applied to *Parachironomus* taxonomy by Paggi (1977), who gives the number of "terminal facets". On the median end of the extension, the pattern of distribution, and number of ommatidia, may vary significantly within a species. Near the transition into the main part of the eye, however, facets were always found in the most dense distribution possible. In this pattern, facet diagonals may be identified extending from ventro-median to dorso-lateral between margins of the eye extension. Consequently, the maximum width of the latter was measured (fig. 1) as the highest number of facets within any of those lateral diagonals reaching the dorsal rim of the eye extension median of an imaginary perpendicular from the inner, frontal corner of the eye to the dorsal margin of the extension. In most cases, dimensions of frontal tubercles could only be given as basal diameters in frontal aspect.

Wing. Paralleling the seam of setae lining the margin of the costa a submarginal row of macrotrichia can be found, whose basal extension proved characteristic in a number of species.

To assess possible variations in the position of RM relative to the wing length, in analogy to the VR (Fittkau 1954) a ratio FV (from German: "Flügel-Verhältnis" = wing ratio) was defined as the length of M (numerator) over the wing length (denominator). Multiplied by 100 the FV gives the distance from RM to the arculus in percent of the wing length.

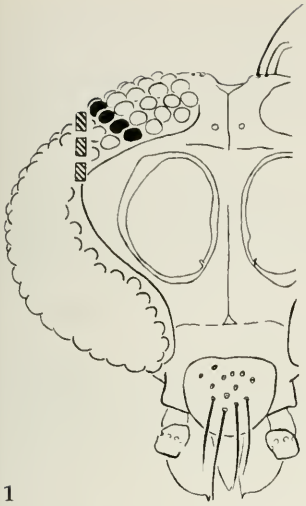
Legs. Wherever possible, species descriptions attempt to define the range of leg segment sizes by giving values for both the largest (left side of each table entry), and the smallest complete specimen available.

Hypopygium. Special slide mounts in lateral aspect were found extremely valuable in elucidating the 3-dimensional morphology of hypopygial structures. In the figures, the gonocoxite/gonostylus pair closer to the viewer is usually omitted for the sake of clarity.

Tab. 1. Most recent catalogues for Chironomidae of major biogeographic regions, and number of species listed for *Parachironomus* Lenz.

Region	Catalog	*Parachironomus* species
Nearctic	Oliver, Dillon & Cranston 1990	16 *
Neotropical	Hunter 1900	–
Palaearctic	Ashe & Cranston 1990	19
Afrotropical	Freeman & Cranston 1980	7
Oriental	Sublette & Sublette 1973	3
Australasian/Oceanic	Cranston & Martin 1989	2

* Does not include 7 new species from Idaho, USA, given by Gillespie 1974 (Ph.D. thesis)



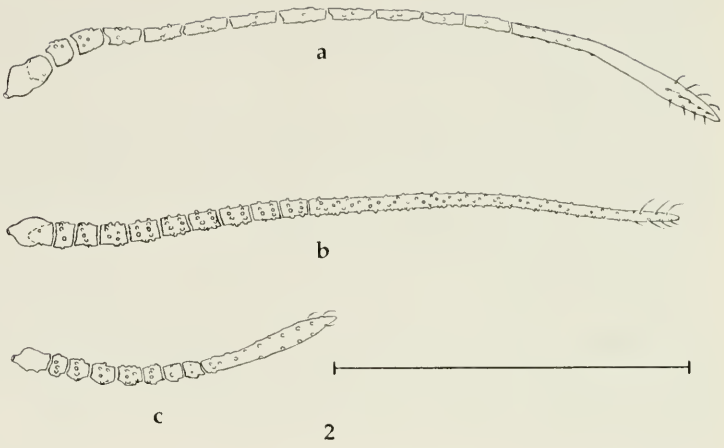


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Fig. 1. Head, frontal view. Facet diagonals of dorsomedian eye extension.
Fig. 2. Antennae of Neotropical *Parachironomus* species. a. *aberrans*, spec. nov.; b. *tirio*, spec. nov., normal male; c. *tirio*, ♂ intersex. Scale: 400 µm.

Generic Diagnosis for the Neotropics

Imago ♂

Very small to medium size, wing length 0.8-2.9 mm.

Coloration variable. Base colour (in alcohol preserved specimens) milky, pale yellow or olive to dark brown. Vittae always darker; darkened postnotal areas, preepisternum and pleural spot common. Legs without bands, tendency toward darkening increasing from proximal to distal segments, and from hind to fore leg.

Head. 5-22 temporals in 1 or 2 rows. Eyes bare, with dorsomedian extension containing either 5 or 6 ommatidia in each lateral facet diagonal. Frontal tubercles present or absent. Antenna (fig. 2) with 11 flagellomeres, *aberrans* with 13; AR = 1.0-2.6, *aberrans* = 0.45. Clypeus with 10-26 setae. 5 palpomeres, regularly increasing in length from p_2 to p_5; palpomeres 3-5 comparatively short in *mirim*, $p_3 = p_4$ in *waika*.

Thorax. Antepronotum grooved, not completely cleft. Scutal tubercle present, rarely very low. 4-18 acrostichals, 1 row on each side of median suture, extending from far oral to scutal tubercle. 4-13 dorsocentrals in each simple lateral row. 3-6 prealars each; 2, widely separated, in *mirim*. 2-19 scutellars in 1 or 2 transverse rows, if in 2, then anterior setae fewer and weaker.

Wing. Membrane usually bare, with numerous macrotrichia in *puberulus*, *vistosus*. Veins R, R_1, and at least distal half of R_{4+5} with macrotrichia, only Sc and M always bare; a row of submarginal macrotrichia on C extending from R_{4+5} at least to R_1 *(osa)*, generally to near RM; vein macrotrichia very sparse in *mirim*. C ending at R_{4+5}, R_{2+3} ending within proximal third of distance R_1 to R_{4+5}. M shorter than 1/2 wing length, FV = 0.38-0.46. Cu longer than M, VR = 1.12-1.35. Squama fringed to bare.

Legs. Apex of fore tibia bearing rounded scale. Mid legs each with 2 tibial combs adjacent, slightly asymmetrical, inner combs wider. Hind tibial combs, 2 per leg, adjacent or narrowly separated, highly asymmetrical, inner combs much wider; hind tibial combs fused in *mirim*. Tibial spurs variable (intraspecifically in *supparilis*), very long to absent, usually 1 spur per comb; outer spur often shorter, on hind tibiae the inner spur set near the end of its comb close to the other comb; tips of spurs often curved; *mirim* with only one spur per leg. LR_1 = 1.45-2.6; LR_2 = 0.5-0.65; LR_3 = 0.6-0.8.

Abdomen. Tergite VIII in one species *(matapi)* with postero-median hump densely covered with strong to medium setae.

Hypopygium. Anal tergite bands of weak V- to Y-type, often separated medially, median longitudinal band long to absent. Caudal region of anal tergite with or without lateral or latero-ventral projections. Anal point size, shape, and region of origin very variable among species. Setation of anal tergite usually extending from around base of anal point to lateral and somewhat ventral, additional dorsomedian setae common; ventralmost setae usually pointing to ventral; *manaos*, *puberulus*, and *vistosus* with conspicuous, separate ventral setal groups.

Superior volsella in dorsal view generally rod-shaped, slender, straight to slightly sinuous; distal part often bending to dorsal, slightly to distinctly widened, sometimes with median extension giving pediform appearance; distal region with two setae arising from bases located in separate, small and shallow to large and deep pits; usually, one pit smaller and in more median, subapical to slightly proximal position; superior volsellae of *tirio* and *atroari* with unique details.

Inferior volsella pubescent, but without setae; rarely reaching beyond anal tergite, with bluntly rounded to fairly acute median to caudal projection. Gonocoxite with 3-5 medio-basal setae.

Gonostylus straight, or turning, curving or bending to median and/or dorsal; basal to distal circumference changes - especially in lateral view - very variable; basal region bare, with few isolated setae, or lateral setal patch extending over entire gonostylus; 2-7 medio-distal setae in often characteristic distribution; 1 subapical dorsal seta present or absent; frequently, 1 of several rows of median setae continuing ventral of medio-distal setae to subapical point on lateral margin of gonostylus.

Key to the male imagines of *Parachironomus* Lenz of the Neotropical faunal region

1. Superior volsella short and thick. Diagonals of dorsomedial eye extension with at most 3 facets. Tibial spurs absent ..... *robustus* Paggi
– Superior volsella at least partially slender. Eye extension diagonals of up to 5 or 6 facets ..... 2.
2. Lateral diagonals of eye extension containing 5 facets each. Squama with setae. Distal part of gonostylus curving or bending to median ..... 3.
– Lateral diagonals of eye extension of 6 facets each. If squama with setae, then gonostylus straight .... 5.
3. Wing macrotrichia on veins only. Frontal tubercles conspicuous .... *supparilis* (Edwards) superspecies !
– Wing membrane with macrotrichia. Frontal tubercles absent ..... 4.
4. Anal tergite with prominent caudo-lateral projections (Fig. 36). Superior volsella pediform .... *vistosus* Paggi
– Anal tergite without projections. Superior volsella rod-shaped (Figs 22, 23) .... *puberulus* (Edwards)
5. Anal point very slender, ca. 2/3 of gonostylus in length (Fig. 33). Squama with setae .... *ticuna*, spec. nov.
– Not as above ..... 6.
6. Distal part of superior volsella with lateral projection bearing spicules (Figs 34, 35) .... *tirio*, spec. nov.
– Superior volsella without spicules ..... 7.
7. Mid and hind tibiae with 1 spur only. Wing veins with very few macrotrichia .... *mirim*, spec. nov.
– Mid and hind tibiae with 2 spurs each. Numerous macrotrichia on R, R_1, R_{4+5} ..... 8.
8. Caudal region of anal tergite with ventrolateral projections, reaching far caudal of wide, triangular, dorsal origin of anal point ..... 9.
– Not with above combination ..... 13.

9. Anal point very wide over entire length. Superior volsella without distal widening, dorso-distal setal pit very small ..... *apalai*, spec. nov.

– At least mid region of anal point distinctly narrowed. If distal part of superior volsella little widened, then dorsal setal pit conspicuous ..... 10.

10. Anal tergite at most with 3 setae dorsally, on base of anal point. Gonostyli curving to median ..... 11.

– Anal tergite with numerous dorsomedian setae. Gonostyli in dorsal view nearly straight ..... 12.

11. Tergite VIII with postero-median setaceous hump. Gonostylus with disto-median dorsal overlap (Figs 16, 17) ..... *matapi*, spec. nov.

– Tergite VIII without hump. Gonostyli evenly curving, without disto-median ventral recess ..... *camajura*, spec. nov.

12. Superior volsella slender, with smooth surfaces ..... *yanomani*, spec. nov.

– Superior volsella distally enlarged, ringed by folds below dorsal setal pit (Figs 6, 7) ..... *atroari*, spec. nov.

13. Gonostylus somewhat truncate, abruptly narrowing beyond subapical dorsal peak (Figs 10, 11, 13, 14) ..... 14.

– Distal region of gonostylus tapering slightly and gradually ..... 15.

14. Dorsomedian setae of anal tergite forming a patch. Superior volsella distally widened (Fig. 13). Base of gonostylus with lateral seta ..... *guarani*, spec. nov.

– Dorsomedian setae of anal tergite in pair of rows (Fig. 10), or very sparse. Superior volsella without widening. Base of gonostylus bare ..... *cayapo*, spec. nov.

15. Antenna with 13 flagellomeres (Fig. 2a). Squama with setae ..... *aberrans*, spec. nov.

– Antenna with 11 flagellomeres. Squama bare ..... 16.

16. Anal tergite without dorsal setae, in ventromedian position with a conspicuous pair (Fig. 15b) ..... *manaos*, spec. nov.

– Not with above combination ..... 17.

17. Base of anal point very broad, reaching far beyond anal tergite (Fig. 37). Costal submarginal macrotrichia extending basally past RM ..... *waika*, spec. nov.

– Base of anal point not as above. Costal submarginals extending from R_{4+5} to R_1 ..... *osa*, spec. nov.

Parachironomus aberrans, spec. nov.

Figs 2a, 3

Etymology. The name has been chosen to represent the occurrence of antennae with 13 flagellomeres, a feature so far unique in the whole *Harnischia* complex of genera.

Imago ♂ (compare table 3)

Size. Small, body length estimated at ca. 3 mm (n=1), wings missing on holotype.

Colour (in Canada balsam). Thorax dark olive brown, vittae and parts of postnotum slightly darker.

Head. Postocular regions largely broken off, temporals probably partially missing; antenna (fig. 2a) with 13 flagellomeres exhibiting relatively few setal bases; segments 4-12 each significantly longer than those of any other *Parachironomus* studied; palpi partially missing.

Wings. Missing; 2 squamals (squama attached to thorax).

Legs. Only two segments of hind leg preserved. fe = 640, ti = 650 µm; tibial spurs broken off.

Hypopygium (Fig. 3). Anal tergite bands of Y-type; median longitudinal band thin, not connected to

transversals. Caudal region of anal tergite without lateral projections. Anal point slender, distal part little widened; anal tergite with 14 setae: dorso-caudally, around base of anal point, and caudo-laterally to ventrally; in ventral position, a row of three setae on each side (as illustrated for *P. directus* by Dendy & Sublette (1959), Fig. 13).

Superior volsella tapering from stout base to slender, straight stem; distal part slightly widened, projecting to median; setal pits of about even size, situated disto-laterally and proximo-medially on distal part of superior volsella.

Inferior volsella with blunt projection more mesal than caudal, not reaching beyond caudal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus almost straight, comparatively long and slender, apex moderately pointed; gonostylus with 2 long setae basally, 5 medio-distal setae, and 1 subapical dorsal seta.

Types. Holotype: ♂ imago, Venezuela, ca. 100 km W of Caracas, kinon, August 1962, leg. E. J. Fittkau. Slide mounted in Euparal (Zoologische Staatssammlung, München - ZSM).

Distribution and ecology. The single specimen was skimmed off the surface of a small, concrete reservoir. Because of its very poor condition (partial decay before sample collection), its original habitat is considered unclear.

Remarks

The hypopygium of *aberrans* is very similar to that of *Parachironomus directus* (Dendy & Sublette 1959: 514), so far known only from several southern USA states. The apex of the gonostylus appears more blunt in *directus*, the anal point slightly longer and without distal widening.

For a detailed comparison, published descriptions of *directus* (Dendy & Sublette 1959, Beck & Beck 1969) were studied, as well as a reference slide mount in the collection of the ZSM (USA, New Mexico, Eddy County, Harroun Canal, Pecos River, at light, 18/5/1979, collector unknown, from the collection of Prof. J. E. Sublette). Apart from the number of flagellomeres, and the above mentioned hypopygial traits, no further reliably separating characters could be found.

Within the *Harnischia* complex of genera, intraspecific variation of the number of flagellomeres so far has only been encountered in connection with parasite-induced intersexuality (compare "Remarks" to *P. tirio*). The flagellomeres of *aberrans* also differ in shape and setation from those known for other *Parachironomus*. On the other hand, no evidence exists for potential erroneous misassociation of body parts on the holotype mount. Therefore, *Parachironomus aberrans* is established here as a species separate from *directus* based on its unique antennal structures.

Differential diagnosis. *Parachironomus aberrans* differs from all other known species in its genus by possessing antennae with 13 flagellomeres. Within the Neotropics, the combination of squamae with setae, and an anal point shorter than 1/2 the length of the gonostylus is distinctive. In contrast to the Nearctic *P. directus* (Dendy & Sublette), *aberrans* shows a more pointed apex of the gonostylus, and a slight distal widening of the anal point.

Parachironomus apalai, spec. nov.

Figs 4, 5

Imago ♂ (compare table 3)

Colour (in Canada balsam). Base colour brownish olive, vittae brown.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	490	320	700	345	260	200	80
P_2	460	390	225	115	80	45	25
P_3	520	490	350	180	150	80	40

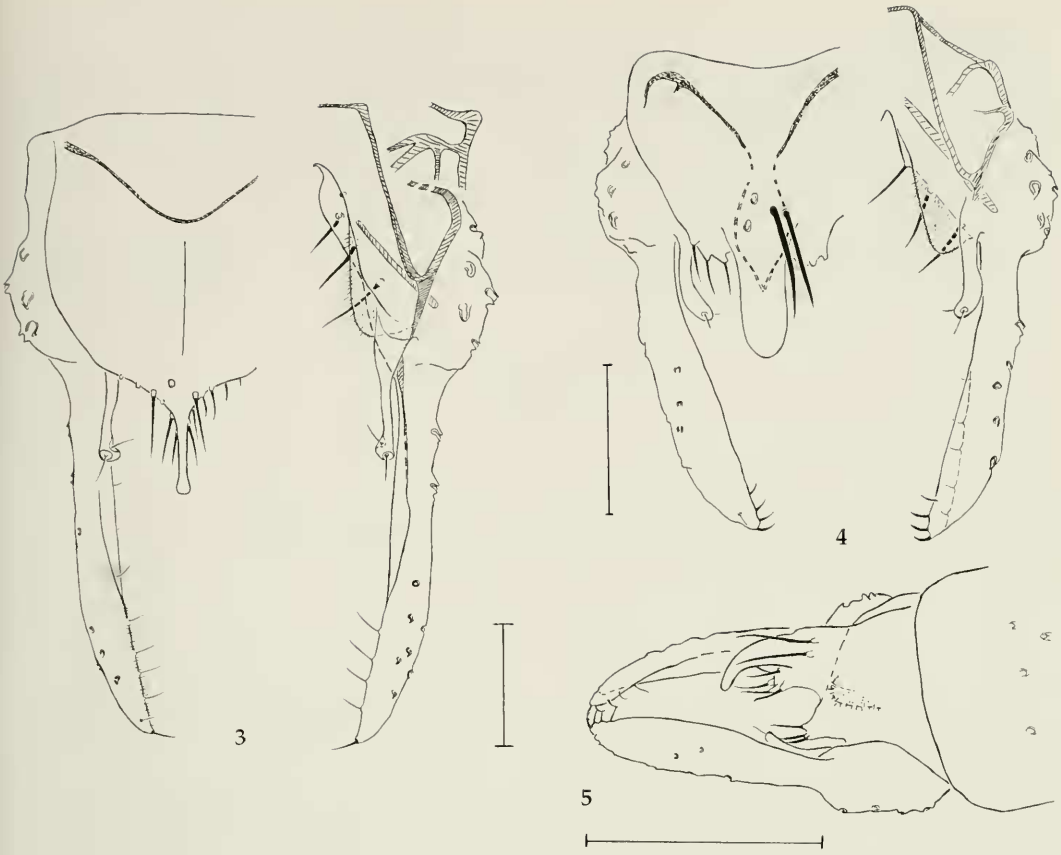


Fig. 3. *Parachironomus aberrans*, spec. nov. Hypopygium, dorsal view. Scale: 50 µm.
Figs 4-5. *Parachironomus apalai*, spec. nov. Hypopygium. 4. Dorsal view. 5. Lateral view. Scales: 50, 100 µm.

Hypopygium (Figs 4, 5). Anal tergite bands of unique type (Fig. 4), in dorsal view embracing dorsomedian setae of anal tergite, and meeting inside base of anal point. Caudal region of anal tergite with lateral projections. Anal point in dorsal view originating anterior of caudal margin of anal tergite; very broad from slightly wider base to smoothly rounded apex; anal point in lateral view (Fig. 5) with basal lobe, curving to deeply ventral distally. Anal tergite with 4 dorsomedian setae, 3 setae arising from bases markedly protruding from basal lobe of anal point, and 3 setae on each lateral projection.

Superior volsella slender, somewhat sinuous; distal region not distinctly widened, curving slightly to median; setal pits small and shallow, situated on opposite sides (dorsal and ventral) of distal part of volsella.

Inferior volsella with moderately pointed medio-caudal projection. Gonocoxite with 3 medio-basal setae.

Gonostylus stout, almost straight, narrowest at base, and little widening in either dorsal or lateral aspect; distal half of stylus with dorso-median contour overlapping ventro-median contour; basal region without setae; 4 medio-distal setae, 1 subapical dorsal seta.

Types. Holotype: ♂ imago, Brazil, Pará, Rio Parú de Oeste, Mission Tiriyos, at light, 29/3/1962, leg. E. J. Fittkau. Slide mounted in Canada balsam, to be deposited at INPA, Manaus, Brazil.

Originally, the hypopygium had been mounted in lateral orientation. After drawing the specimen in this aspect, the medium was re-softened in a xylene chamber, and the hypopygium rotated into its present dorsal aspect position.

Distribution. The only known specimen was taken at about 400 m altitude, in the northern Amazon peripheral region, near the border with Surinam.

Remarks

The holotype of *apalai* represents only the second *Parachironomus* species so far collected in the upper Rio Parú region. All other samples taken there contained *P. tirio* exclusively. In this context, it is interesting to note, that both the holotype of *apalai*, and the vast majority of specimens of *tirio* in these collections taken at lights, were found to contain a Nematode parasite.

In light of the possible consequences of parasitism discussed in the "Remarks" to *P. tirio*, the character data derived from the single individual of *P. apalai* must be considered preliminary.

Differential diagnosis. The shape of the anal point, which is very wide over its entire length, distinguishes *apalai* from all other *Parachironomus* known so far.

Parachironomus atroari, spec. nov.

Figs 6, 7

Imago ♂ (compare table 3)

Colour (in alcohol). Appears strongly faded in all specimens seen. Thorax pale yellowish brown; darkening of vittae and postnotal areas faintly noticeable. Legs uniformly pale whitish.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	715/640	440/390	960/840	480/445	370/340	280/265	125/120
P_2	640/570	560/475	310/285	170/150	130/110	70/ 65	45/ 40
P_3	730/640	690/620	505/445	230/225	210/195	130/115	70/125

Tibial spurs comparatively very long, up to about five times the height of associated tibial comb. Hind legs with tips of spurs on longer combs bent outward.

Hypopygium (Figs 6, 7). Anal tergite bands of V- or Y-type; median longitudinal band, if present, with caudal split embracing most proximal dorsomedian setae of anal tergite. Caudal region of anal tergite with lateral projections. Anal point in dorsal view originating anterior of caudal margin of anal tergite; base broadly triangular, wider at origin than moderately widening distal part; stem of anal point in lateral view (Fig. 7) as wide (on a dorso-ventral axis) as base; ventral contour of stem with several notches, meeting ventral side of distal widening near ventral end of the latter; anal point directed straight to caudal, only disto-dorsal widening part bending obliquely to ventral. Anal tergite with ca. 20-35 (n=4) setae: dorsomedially, around base of anal point, and dorsally to ventrally on caudo-lateral projections of anal tergite.

Superior volsella stout, widest in distal part; stem directed straight to caudal, distal part in lateral view (Fig. 7) bending to dorsal at about right angle to stem; distal part ringed with conspicuous folds below large and deep disto-dorsal setal pit; median pit at base of distal part of volsella.

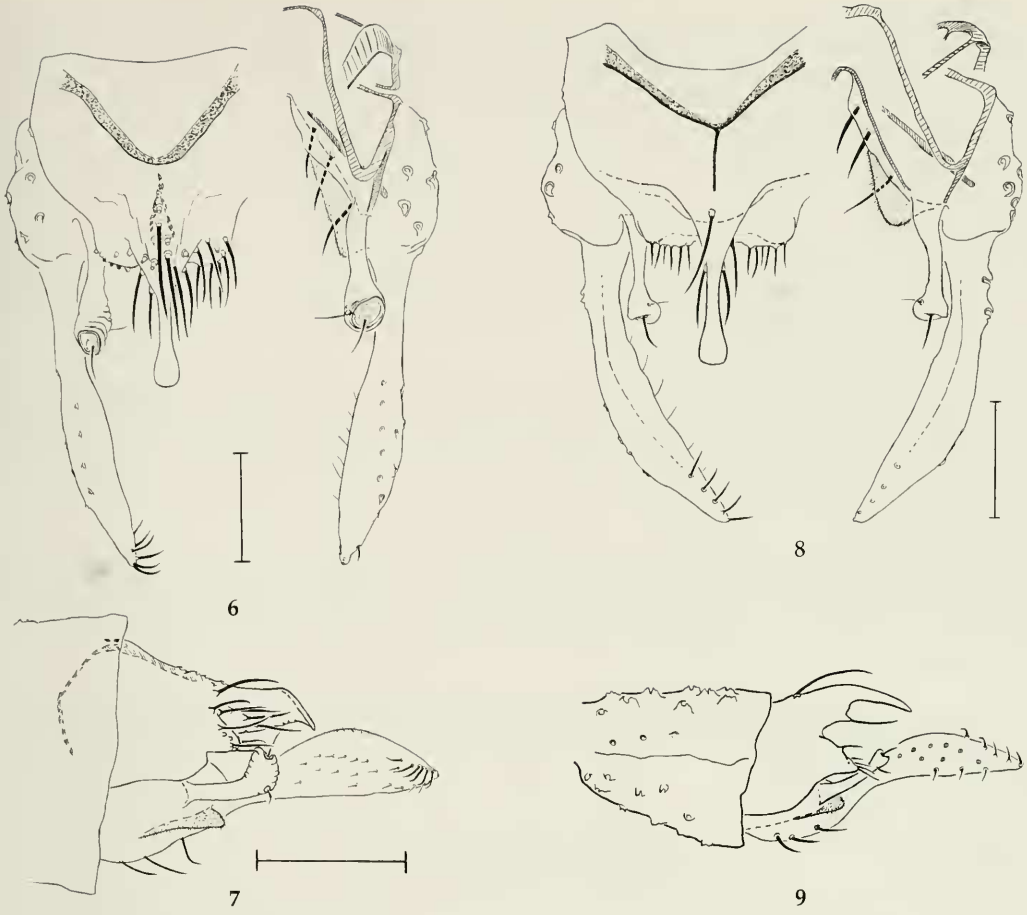
Inferior volsella with moderately to fairly acute medio-caudal projection, occasionally reaching beyond anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus narrowest just distal of base, in dorsal view only little widening in distal half; in lateral view (Fig. 7) with midsection widening, and moderately pointed apex; narrow base part of gonostylus without lateral setae; 6-8 medio-distal setae, 1 subapical seta in lateral position.

Types. Holotype: ♂ imago, Brazil, Amazonas, Ilha do Careiro, Paraná da Terra Nova, ca. 2 km above mouth, at light, 15/3/1961, leg. E. J. Fittkau, slide mounted in Canada balsam (to be deposited at INPA, Manaus, Brazil). - Paratypes (Brazil, Amazonas). 1♂ imago, Rio Negro, "just below confluence of Igarapé Bica", 23/6/1961, leg. E. J. Fittkau; 1♂ imago, locus typicus, all data as for holotype; 3♂♂ imagines, Ilha do Careiro, Lago do Rei, at light on a boat, 28/9/1959, leg. Sioli-Sattler, slide mounted in Canada balsam (ZSM).

Further record. Brazil, Amazonas, lower Rio Madeira, Paraná Madeirinha, 11/9/1960, leg. E. J. Fittkau.

Distribution and ecology. The few collection sites are all located near larger bodies of water within a limited central Amazon lowland area around Manaus.



Figs 6-7. *Parachironomus atroari*, spec. nov. Hypopygium. 6. Dorsal view. 7. Lateral view. Scales: 50, 100 µm.
Fig. 8-9. *Parachironomus camajura*, spec. nov. Hypopygium. 8. Dorsal view. 9. Lateral view. Scales: 50, 100 µm.

Differential diagnosis. *Parachironomus atroari* joins a group of species with caudo-lateral projections of the anal tergite. Among these forms, *atroari* stands out by its distally stout superior volsellae ringed with conspicuous folds.

Parachironomus camajura, spec. nov.

Figs 8, 9

Imago ♂ (compare table 3)

Colour (in alcohol). Thorax faintly brownish olive, vittae and postnotum (often weakly) light brown; legs mostly pale, 1 specimen with brownish fore tarsi.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	550/470	335/285	745/640	375/310	275/240	195/165	85/75
P_2	450/410	415/375	235/205	120/ 90	85/ 65	45/ 40	30/30
P_3	560/480	560/470	365/305	185/140	150/115	85/70	45/40

Hypopygium (Figs 8, 9). Anal tergite bands of Y-type; anal tergite with caudal projections, lateral and ventral of base of anal point; lateral corners of projections each with another low dorsal lobe. Anal point in

dorsal view originating far anterior of caudal contour of anal tergite; base of anal point long, triangular; distal part of anal point moderately widened; anal point in lateral view (Fig. 9) with weak anal lobe, stem and distal part a long, little narrowing spur pointing almost straight to caudal. 1 long seta dorsally on base of anal point, and 2-3 setae on prominent papillae arising from basal lobe of anal point; ventro-lateral projections of anal tergite each with 4-6 setae, including one on dorsal sublobe.

Superior volsella weakly sinuous; stem very slender; distal part enlarged, with median protrusion; disto-dorsal setal pit shallow; second pit on proximal side of median protrusion of distal part of volsella, small to indistinct.

Inferior volsella with blunt medio-caudal projection, not reaching beyond caudo-lateral protrusions of anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus curving to median, narrowest slightly distal of base, midsection widened in lateral view; proximal half of stylus with only 1-2 strong lateral setae, and 5-6 medio-distal setae, situated on dorsal edge of apical region; subapical dorsal seta absent.

Types. Holotype: ♂ imago, Colombia, Meta, Mozambique, at light, 6/3/1971, leg. S. S. Roback (ZSM). - Paratypes (Brazil): 1♂ imago, Amazonas, Lago Cabaliana at Manacapurú, in vegetation, 9/11/1971, leg. F. Reiss; (Mato Grosso): 1♂ imago and 3♂♂ hypopygia, Igarapé Garapu, upper reaches ("at camp I"), at light, 24-27/8/1965, leg. E. J. Fittkau; 1♂ imago, hypopygium lost, Rio 7. Setembro, at light, 28/8/1965, leg. E. J. Fittkau. All type material slide mounted in Euparal (ZSM).

Distribution and ecology. The few known specimens of *P. camajura* have been collected from two peripheral regions of Amazonia, and from a central Amazon várzea lake of mixed water type. These findings indicate that *camajura* is distributed throughout the tropical lowlands of northern South America, but does not develop in biotopes extremely poor in electrolytes. For limnological data see Roback & Nieser (1974; locus typicus), and Reiss (1976).

Differential diagnosis. Among the species with caudo-lateral projections of the anal tergite, *camajura* is distinguished by dorso-lateral sublobes of these projections, and by gonostyli curving evenly to median from just distal of their bases.

Parachironomus cayapo, spec. nov.

Figs 10-12

Imago ♂ (compare table 3)

Colour (in alcohol). Base colour pale to olive; head and vittae usually brownish.

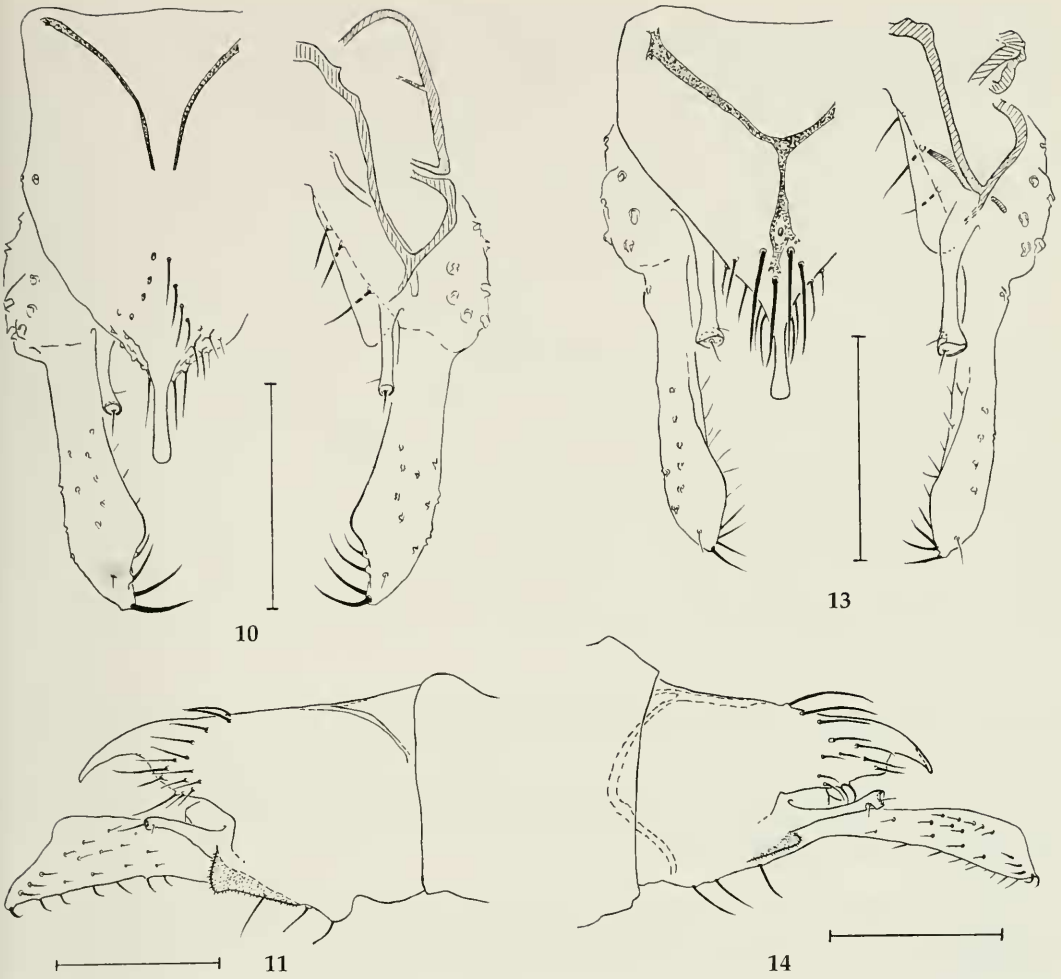
Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	770/610	480/380	1010/820	490/410	370/310	280/230	120/100
P_2	680/535	600/490	340/280	160/190	120/100	70/ 60	45/ 35
P_3	790/620	750/590	550/445	260/210	220/180	120/100	60/ 60

Hypopygium (Figs 10, 11). Anal tergite bands usually forming an open "V", short median longitudinal band rarely present. Caudal region of anal tergite without lateral projections. Anal point originating from or near caudal margin of anal tergite, slender, with little distal widening; anal point in lateral view (Fig. 11) with at most low basal lobe, dorsal and ventral contours evenly curving to ventral. Anal tergite with ca. 15-30 setae, dorsomedian setae usually in pair of opposite rows, laterally running into patches from base of anal point to lateral and ventral; single specimens from Costa Rica and Surinam with only 2 dorsomedian setae in isolated anterior position.

Superior volsella very slender, straight, directed to caudal or - sometimes only 1 per specimen - oriented to median, paralleling caudo-lateral margin of anal tergite; distal part of volsella not widened; disto-dorsal setal pit distinct, median pit small, usually in distinctly proximal position.

Inferior volsella with moderately to fairly acute caudal projection, sometimes reaching slightly beyond anal tergite. Gonocoxite with 3 medio-basal setae.



Figs 10-11. *Parachironomus cayapo*, spec. nov. Hypopygium. 10. Dorsal view. 11. Lateral view. Scales: 100 µm.
Figs 13-14. *Parachironomus guarani*, spec. nov. Hypopygium. 13. Dorsal view. 14. Lateral view. Scales: 100 µm.

Gonostylus narrowest at base, straight, widening to prominent dorso-median lobe just proximal of apex; gonostylus in lateral view (Fig. 11) comparatively wide on dorso-ventral axis, and with protruding disto-dorsal hump; basal region without lateral setae; 3-4 medio-distal setae, leading from apical, protruding knob into a field of weaker medio-basal setae; 1 subapical dorsal seta.

Types. Holotype: ♂ imago, Colombia, Meta, Mozambique, at light, 6/3/1971, leg. S. S. Roback. Slide mounted in Euparal (ZSM).

Paratypes: 1♂ imago, Costa Rica, Osa, Rancho Quemado, at light, October 1990, collector unknown, from coll. H. W. Riss; 1♂ imago, Surinam, Paramaribo, 17-21/8/1969, leg. N. Nieser. Slide mounted in Euparal (ZSM). - Brazil, leg. E. J. Fittkau - Amazonas: 1♂ imago, Cachoeira Castanha, off Rio Negro ca. 80 km above Manaus, at light, 29/12/1960; 1♂ imago, Rio Negro, "opposite refinery few km from Rio Solimões", at light, 17/3/1961; 1♂ imago, Rio Solimões, 20 km above Igarapé Uarini, at light, 4/9/1961; 1♂ imago, Rio Solimões, 15-20 km below Coari, kinon, 14/9/1961; 1♂ imago, Paraná Madeirinha, at light on boat, 11/11/1960; 3♂♂ imagines, Rio Madeira, ca. 2 hs. before confluence Amazonas, at light, 29/11/1960; - Pará: 2♂♂ imagines, Santarém, inside Hotel Oriental, at light, January 1961; 1♂ imago, Rio Tapajós, near Barra do São Manuel, at light, 13/1/1961; 1♂ imago, lower Rio Tocantins near Marabá, 5/11/1960. Slide mounted in Canada balsam (ZSM). - 5♂♂ imagines, Brazil, Pará, Rio Amazonas, port of Alenquer, at light on boat, 8 P.M., 15/7/1946, leg. Sioli. Slide mounted in Canada balsam (ZSM).

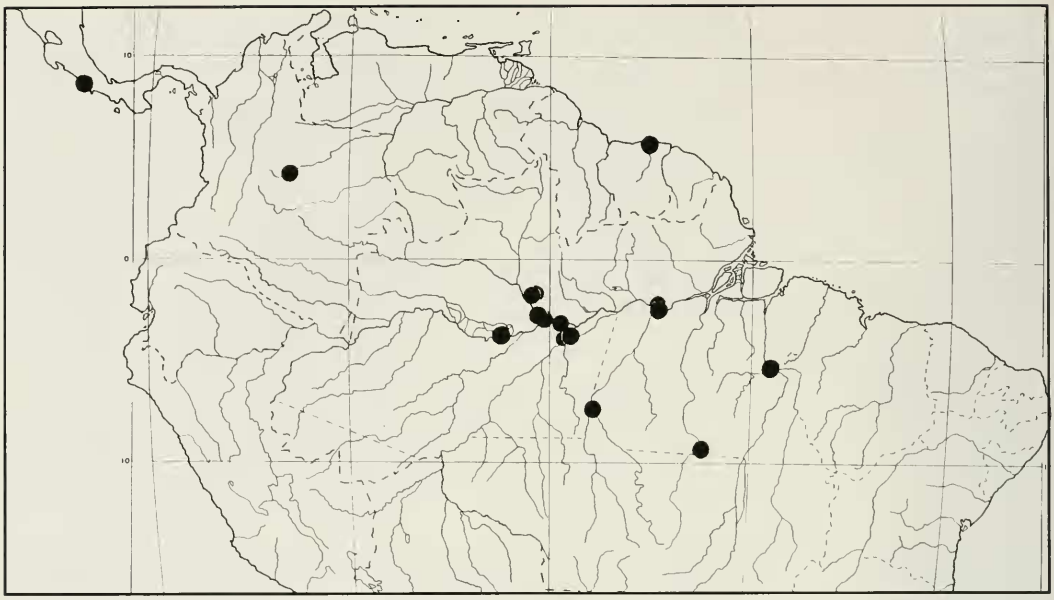


Fig. 12. *Parachironomus cayapo*, spec. nov. Distribution map.

Further records (Brazil, leg. E. J. Fittkau, at light): Amazonas: Rio Preto, Tiririca, at light, 7/7/1962; lower Igarapé do Cachoeira, 27/7/1965; Igarapé do Cachoeira, at confluence Rio Cuieiras, 29/7/1965; Rio Madeira, Borba, 23/10/1965; - Mato Grosso: Igarapé Garapu, "near camp I", 24-27/7/1965.

Distribution (Fig. 12) and ecology. According to the above records, *P. cayapo* may be distributed not only throughout tropical South, but even into Central America. The variety of ecotypes represented does not allow any ecological interpretations.

Differential diagnosis. The truncate shape of the gonostylus separates *cayapo* from all other Neotropical *Parachironomus* species except *guarani* and *ticuna*. Among the latter, *cayapo* is recognized by the combination of squamae without setae, anal point shorter than $^1/_2$ gonostylus length, and superior volsellae without distal widening.

Parachironomus guarani, spec. nov.

Figs 13, 14

Imago ♂ (compare table 3)

Colour (in alcohol). Base colour milky to pale olive; vittae, fore legs from tips of femora, mid legs beginning with ta_2, and hind legs beginning with ta_3: brownish olive.

Legs. Lengths of segments in µm (values on right: holotype):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	660/560	420/360	890/740	500/400	380/300	280/230	120/110
P_2	600/510	510/430	330/270	170/130	120/110	70/ 60	40/ 35
P_3	700/590	700/570	510/430	260/200	220/180	130/100	70/ 55

Hypopygium (Figs 13, 14). Anal tergite bands of Y-type, median connection usually weak; longitudinal band often distally forming a mesh around bases of proximal dorsomedian setae of anal tergite, but entire band occasionally weak or absent. Caudal region of anal tergite without lateral projections. Anal point originating from caudal margin of anal tergite, slender, with slight to moderate apical widening; anal point

in lateral view (Fig. 14) with basal lobe, and (mostly dorsal contour) curving to ventral. Anal tergite with ca. 15-25 setae, distributed over a patch dorsomedially, around base of anal point, and laterally to ventrally.

Superior volsella straight to slightly bent, directed to caudal, with generally distinct distal widening; both distal setal pits conspicuous, median pit in only slightly subapical position; rim of disto-dorsal pit sometimes with hint of proximo-lateral projection.

Inferior volsella with moderately acute caudal projection, not reaching beyond caudal margin of anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus narrowest beyond base bearing 1-2 lateral setae, straight, widest just proximal of bluntly pointed apex; distal region in lateral view (Fig. 14) appearing more or less roundedly truncate; 4-5 medio-distal setae, arranged in a row curving from apex of gonostylus toward dorsal; 1 subapical dorsal seta in fairly lateral position.

Types. Holotype: ♂ imago, Brazil, Amazonas, Paraná da Terra Nova, "ca. 2 km from mouth", at light, 15/3/1961, leg. E. J. Fittkau, slide mounted in Canada balsam (to be deposited at INPA, Manaus, Brazil). - Paratypes: Brazil, Amazonas, leg. E. J. Fittkau - 2♂♂ imagines, Rio Negro, just below confluence Igarapé Bicá, kinon, 23/6/1961; 1♂ imago, Rio Solimões, near confluence Rio Takana, at light, 15/8/1961; 5♂♂ imagines, all data same as Holotype; 3♂♂ imagines, Paraná Madeirinha, at light, 12/9/1960; 1♂ imago, Rio Tupani, "at 2nd surveying station", 14-15/9/1960; 1♂ imago, Rio Luna Acu, "sampling station 22", at light, 25/9/1960. Slide mounted in Canada balsam (ZSM). - Brazil, Amazonas - 1♂ pupa, lower Rio Solimões, Lago do Calado at Manacapuru, 1968, leg. W. Junk; 1♂ imago, lower Rio Solimões, Lago do Calado at Manacapuru, mass rearing from sediment sample, 30/1/1972, leg. F. Reiss; 1♂ imago, Paraguay, Rio Ypané, at light, 28/9/1985, leg. K. Boettger. Slide mounted in Euparal (ZSM).

Further records (Brazil, Amazonas, leg. E. J. Fittkau): Rio Solimões, ca. 15 km below Coari, at light, 13/9/1961; Rio Madeira, Caranapatuba, 20/10/1965; Bolivia, Beni savanna, 13° S, 220 m altitude, /2/1980, leg. U. Nolte.

Distribution and ecology. *P. guarani* has been collected near larger bodies of water in the central Amazonian lowland region near Manaus, Brazil. The only exceptions so far are one specimen each from Rio Ypané, Paraguay, and the Beni savanna of Bolivia.

One male pupa, and one adult male have been reared out of sand and clay sediment taken at 30 cm depth from an inundated meadow at Lago do Calado on the lower Rio Solimões.

Remarks

A high proportion of the specimens of *P. guarani* examined each contained a Nematode in the abdomen. The discussion of possible consequences on character data given in the "Remarks" to *P. tirio* also applies to the values listed for *guarani*.

Differential diagnosis. The truncate gonostylus separates *guarani* from all Neotropical *Parachironomus* except *cayapo* and *ticuna*. Among the latter, *guarani* may be identified by the following combination: Squama bare, anal point shorter than 1/2 length of gonostylus, superior volsellae with distal widening.

Parachironomus manaos, spec. nov.

Fig. 15

Imago ♂ (compare table 3)

Colour (in Euparal). Base colour light olive brown, vittae darker. Head: Frontal tubercles not discernible, frontal area damaged. Clypeus with few setae (13) relative to body size.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	700	460	–	–	–	–	–
P_2	595	555	315	160	105	60	40
P_3	700	615	555	305	245	140	65

Hypopygium (Fig. 15). Anal tergite bands near Y-type, but all bands widely separated medially, and longitudinal band very weak. Caudal region of anal tergite without lateral projections. Anal point originating from caudal margin of anal tergite, slender, with narrow base and little distal widening. Anal tergite with 11 setae: 1 on each side of base of anal point, 3-4 laterally to ventrally, and 1 pair of large setae in ventro-median positions (Fig. 15b), situated on an apparent ledge posterior of the entrance to the inner genital area.

Superior volsella slightly sinuous, distinctly narrowing from stout base, and with distal widening; proximo-lateral rim of distal setal pit drawn out into low, rounded lobe; median pit in subapical position; dorsal surface of distal region of volsella with short, longitudinal striations.

Inferior volsella with moderately acute caudal projection, not reaching beyond anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus straight, narrowest in mid region, but width in dorsal aspect varying little, distal region appears widened on dorso-ventral axis; basal region with 1 lateral seta; 5 medio-distal setae, 1 subapical dorsal seta in disto-lateral position.

Types. Holotype: ♂ imago, Brazil, Amazonas, lower Igarapé do Cachoeira, at light, 27/7/1965, leg. E. J. Fittkau, slide mounted in Euparal (to be deposited at INPA, Manaus, Brazil).

Ecology. For information on the type locality, see Walker (1987).

Differential diagnosis. *Parachironomus manaos* is recognized by the following combination of characters: Anal tergite without lateral projections, lacking setae in dorsal positions, but with a conspicuous ventral pair situated on an apparent ledge posterior to entrance of inner genital area.

Parachironomus matapi, spec. nov.

Figs 16, 17

Imago ♂ (compare table 3)

Colour (in alcohol). Thorax yellow to golden brown, darkening of vittae and postnotum often weak or absent. Legs (holotype) yellowish brown proximally, fore tibia and proximal half of basitarsus brownish, distal half of ta_1 and ta_{2-5} brown; on mid legs ta_{1-3} brownish, ta_{4-5} brown; ta_{4-5} of hind legs brownish.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	595/470	360/260	790/600	400/290	300/245	205/165	90/80
P_2	510/410	440/330	260/195	120/ 90	85/ 65	50/ 40	35/25
P_3	585/455	570/435	380/275	190/140	160/120	85/ 65	45/35

Abdomen. Tergite VIII with medio-caudal hump (Fig. 17) densely covered with medium long setae, and partially overlapping tergite IX.

Hypopygium (Figs 16, 17). Anal tergite bands of Y-type. Caudal region of anal tergite with lateral projections. Anal point in dorsal view originating far anterior of caudal margin of anal tergite; broad, triangular base making up about half of length of anal point; distal part of anal point comparatively long and wide; anal point in lateral view (Fig. 17) with basal elevation above level of tergite IX, moderately arched, with basal lobe and a ventro-median support for dorsally widening distal part ("T-beam" principle). Anal tergite without dorsomedian setae; 3-4 setae around each side of base of anal point; each caudo-lateral projection of anal tergite with 3-4 setae.

Superior volsella slender, straight, with slightly widened distal part terminating in a tapering median projection. Disto-dorsal setal pit shallow; median seta originating in usually very deep excavation of disto-median volsellar projection.

Inferior volsella with moderately acute caudal projection, reaching beyond caudo-lateral lobes of anal tergite. Gonocoxite extending almost as far beyond anal tergite as superior volsella, with 3 medio-basal setae.

Gonostylus narrowest at base, mid section in lateral view (Fig. 17) moderately widened; distal half of stylus with dorso-median contour progressively overlapping ventro-median contour; proximal half with only 1-2 strong lateral setae; 6-7 medio-distal setae, the 4 apical ones closer together; subapical dorsal seta absent.

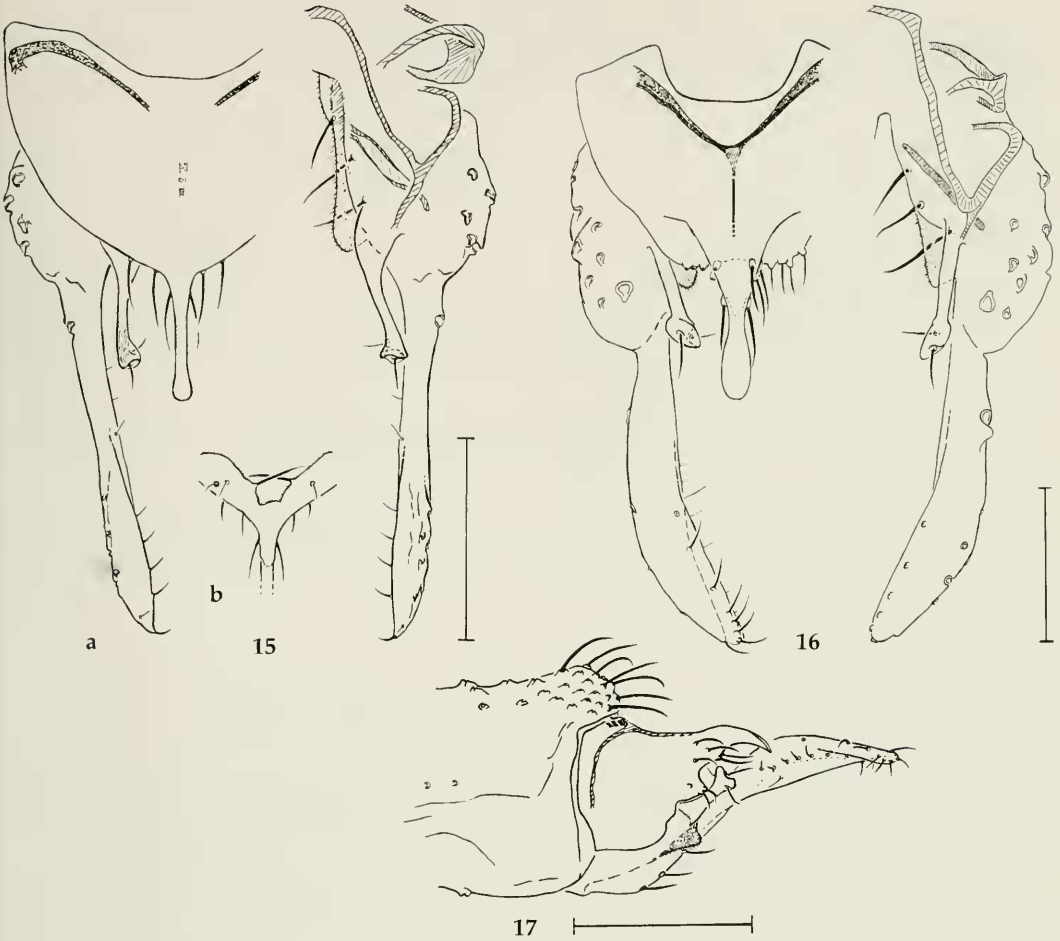


Fig. 15. *Parachironomus manaos*, spec. nov. Hypopygium. a. dorsal view; b. ventral view, detail. Scale: 100 µm. Figs 16-17. *Parachironomus matapi*, spec. nov. Hypopygium. 16. Dorsal view. 17. Lateral view. Scales: 50, 100 µm.

Types. Holotype: ♂ imago, Ecuador, Rio Napo, Laguna Añango, 0°32' S, 76°27' W, at light, 7/9/1988, leg. C. J. Otto, in Euparal (ZSM). - Paratypes: 1♂ imago, Brazil, Território do Rio Branco, Laguna de Magalhães, hand net, 7/12/1971, leg. F. Reiss; (Brazil, Amazonas): 1♂ imago, lower Rio Solimões, Lago do Calado at Manacapurú, mass rearing of sediment sample, 30/1/1972, leg. F. Reiss; 1♂ pupa, Rio Itu, "30 min. above Acampamento II", drift, 14/2/1962, leg. E. J. Fittkau; 1♂ imago, Igarapé Banheiro Mestrinho, km 50 of road to Itacoatiara, kinon, 16/5/1962, leg. E. J. Fittkau, in Euparal; 1♂ hypopygium, Rio Preto, Tiririca, at light, 7/7/1962, leg. E. J. Fittkau; 1♂ imago, Rio Negro, Ilha Marará, at light, 8/2/1962, leg. E. J. Fittkau; 6♂♂ imagines, lower Rio Madeira, Paraná Madeirinha, at light, 12/9/1960, leg. E. J. Fittkau; 3♂♂ imagines, Rio Tupani "at 2nd surveying point", at light, 14-15/9/1960, leg. E. J. Fittkau, in Canada balsam (all ZSM).

Further material examined (Brazil, Amazonas, leg. E. J. Fittkau): Rio Itu, at light, 11/2/1962; lower Igarapé do Cachoeira, at light, 27/7/1963; Igarapé do Cachoeira at mouth, at light, 29/7/1963.

Distribution and ecology. The records point to a widely spread Amazonian distribution. Probable source habitat types include central Amazon white water, as well as extremely electrolyte-poor conditions. Reiss (1973) gives specific conductance values around 5 μS_{20} for a rain-fed depression laguna of the Roraima savannas. One male adult has been reared from sand and clay sediment taken at 30 cm depth from an inundated meadow at Lago do Calado on the lower Rio Solimões.

Differential diagnosis. *P. matapi* is the only known species of its genus bearing a postero-median, setaceous hump on abdominal tergite VIII. The combination of caudo-lateral projections of the anal tergite, and wide anal point with very short narrow midsection is also unique.

Parachironomus mirim, spec. nov.

Figs 18, 19

Imago ♂ (compare table 3)

Size. Very small; wing length 0.79-0.93 mm (M=0.85; n=7), for specimens parasitized by Nematodes (refer to "Remarks") 0.73-0.78 mm (M=0.775; n=6).

Colour (in alcohol). Base colour olive brown, vittae, caudal $^2/_3$ of postnotum, median anepisternal spot, and preepisternum brown; fore legs and joints between femora and tibiae brown, sometimes mid tarsi 2-5 and hind tarsi 4 and 5 also slightly darkened.

Head. Frontal tubercles usually indistinguishable, but minute humps present on a few specimens. Antennae always with 11 flagellomeres, but often with reduced setation and widened terminal segment; AR = 1.03-1.25 (M=1.12; n=7), for parasitized males 0.62-0.90 (M=0.75; n=7). Palpomeres 3-5 comparatively very short.

Wing. Costal submarginal row absent; only very few vein macrotrichia, on R and distal end of R_{4+5}. FV = 0.42-0.43 (n=2); for one parasitized specimen FV = 0.42; VR = 1.21-1.25 (n=2); one parasitized individual with VR = 1.20.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	– /315	190/170	445/405	250/220	195/180	130/120	60/55
P_2	330/315	270/245	155/140	65/ 65	45/ 45	30/ 30	25/25
P_3	370/350	350/310	270/225	140/120	125/110	70/ 60	40/40

LR_1 = 2.16-2.59 (M=2.34; n=5); for parasitized specimens LR_1 = 2.24-2.48 (M=2.38, n=3). LR_2 = 0.56-0.63 (M=0.59; n=7), one parasitized specimen with LR_2 = 0.57. LR_3 = 0.67-0.77 (M=0.725; n=6), one parasitized specimen with LR_3 = 0.73. Hind tibial combs fused, bearing only one tibial spur per leg.

Hypopygium (Figs 18, 19). Transversal anal tergite bands very short and far apart medially, longitudinal band absent. Caudal region of anal tergite with lateral projections. Anal point in dorsal view originating near caudal margin of anal tergite, very slender distal of moderately wide, triangular base, with little apical widening; anal point in lateral view (Fig. 19) without distinct basal lobe, pointing straight to caudal, with little apical curving to ventral. Anal tergite with 8-15 setae, dorso-laterally to below base of anal point.

Superior volsella short and stout, slightly widening distally, in dorsal view directed to caudal, in lateral view with distal part bent to dorso-caudal; disto-dorsal setal pit deep, median pit located at base of distal part of volsella.

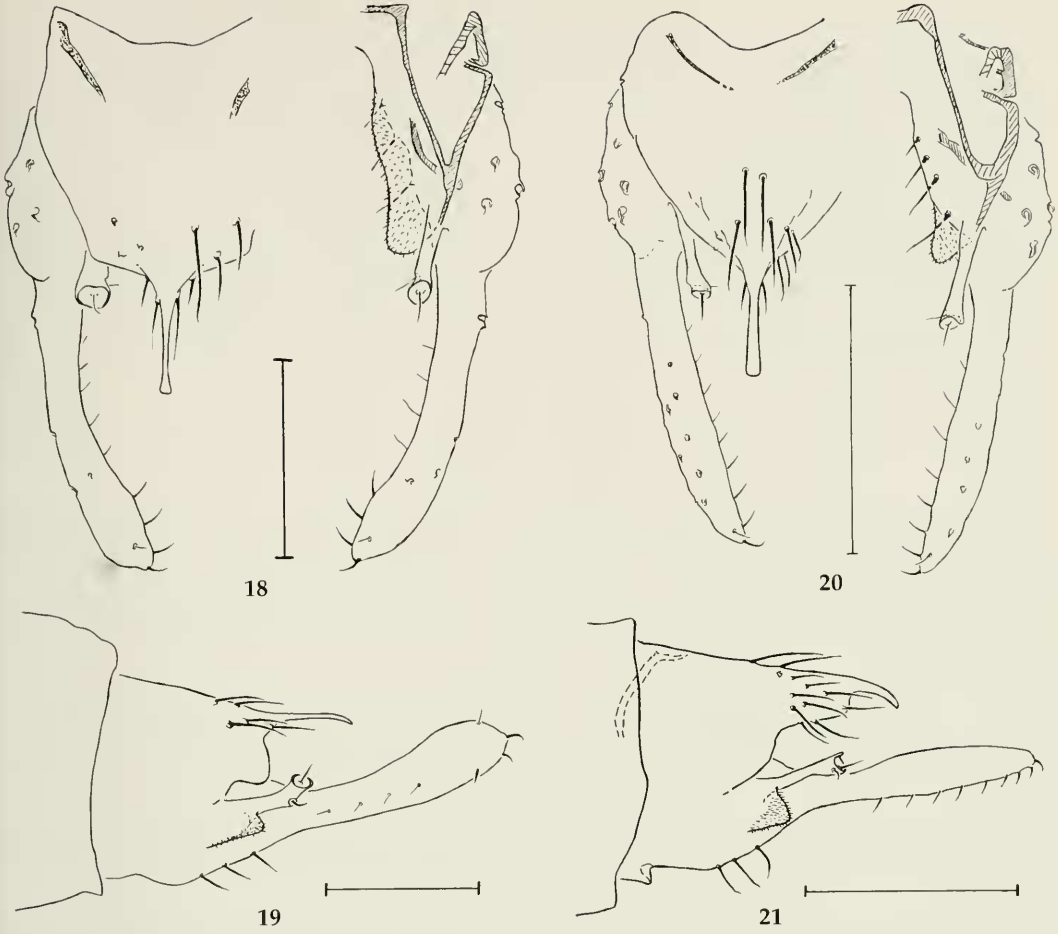
Inferior volsella with blunt to moderately pointed caudal projection, not reaching beyond anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus narrowest beyond base bearing 1 lateral seta, smoothly curving to medio-dorsal, with slight widening just proximal of bluntly pointed apex; 4 medio-distal setae, 1 subapical dorsal seta.

Types. Holotype: ♂ imago, Brazil, Amazonas, Igarapé Cachoeira, near mouth, at light, 26/11/1962, leg. E. J. Fittkau, slide mounted in Canada balsam (to be deposited at INPA, Manaus, Brazil).

Paratypes (Brazil): at light, leg. E. J. Fittkau - Amazonas: 1♂ imago, Igarapé Cachoeira, at confluence Rio Cuieiras, 300 m downstream of type locality, 23/11/1962; 10♂♂ imagines, Rio Tarumãzinho, several km below Sucuuba, 16-17/11/1962. Slide mounted in Canada balsam (ZSM). - Amazonas: 1♂ imago, lower Igarapé Cachoeira, 27/7/1965; 1♂ imago, Igarapé Cachoeira, at confluence Rio Cuieiras, 300 m downstream of type locality, 23/11/1962. - Mato Grosso: 1♂ imago, Lago Cameiura, N of Hukula, 18/9/1965. Slide mounted in Euparal (ZSM). - 1♂ imago, Amazonas, lower Rio Cuieiras, 22/7/1971, leg. F. Reiss. Slide mounted in Euparal (ZSM).

Further records: 1♂ pupa, Brazil, Amazonas, Rio Negro, 2 km below Tapuruquara, kinon, 6/2/1963, leg. E. J. Fittkau.



Figs 18-19. *Parachironomus mirim*, spec. nov. Hypopygium. 18. Dorsal view. 19. Lateral view. Scales: 50 µm.
Figs 20-21. *Parachironomus osa*, spec. nov. Hypopygium. 20. Dorsal view. 21. Lateral view. Scales: 100 µm.

Distribution and ecology. *P. mirim* has mostly been collected in a small central Amazon lowland area NW of Manaus, Brazil, near streams and rivers carrying rather black (organic acid rich) waters. For information on the limnology and ecology of these streams, see Walker (1987). The only exception to this pattern is a single specimen from the upper Rio Xingu area on the southern Amazon periphery. Lago Cameiura holds water of the clear, crystalline type, its shallow, sandy litoral was found covered with a fine layer of mud.

Remarks

In several of the samples taken of *P. mirim*, all specimens collected each contained one Nematode in the abdomen. The character data given above show significant reductions in the AR and, to a lesser extent, wing lengths of the parasitized individuals. Although table 3 gives only data for apparently normal males, the potential influence of parasitism (compare "Remarks" to *P. tirio*) should be kept in mind.

Differential diagnosis. The most distinguishing features of *P. mirim* are the very low number of macrotrichia on veins of the wing, single spurs on each mid and hind tibia, and an anal point extremely slender and almost entirely straight.

Parachironomus osa, spec. nov.

Figs 20, 21

Etymology. The name refers to the Osa peninsula, Costa Rica, harbouring the so far only collection sites of this species.

Imago ♂ (compare table 3)

Colour (in alcohol). Thorax base colour olive, vittae and postnotal patches brown. Abdomen and legs pale, only fore legs brownish from tips of femora to ta_5.

Head. Temporals in a single row. Frontal tubercles small to indistinguishable. Third palpomere comparatively long.

Wings. Submarginal row of setae on costa not reaching much further basal than R_1.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	610	380	790	440	350	–	–
P_2	520	450	290	140	90	60	40
P_3	600	610	440	210	195	120	60

Hypopygium (Figs 20, 21). Transversal anal tergite bands short, fading far apart medially. Caudal region of anal tergite without lateral projections. Anal point long and slender, originating somewhat antero-dorsal of caudal margin of anal tergite; base moderately wide, triangular; distal region not markedly widened; anal point in lateral view (Fig. 21) with basal lobe, beyond the latter a slender spur, moderately curving to ventro-caudal. Anal tergite with ca. 15-25 setae: dorso-medially, around base of anal point, and laterally to ventrally.

Superior volsella slender, pointing straight to caudal; distal part little to moderately enlarged; disto-dorsal setal pit assuming all of distal surface; median pit smaller, in only slightly subapical position; proximo-lateral rim of distal setal pit often drawn out into a low rounded projection.

Inferior volsella with comparatively narrow base and moderately acute caudal projection. Gonocoxite with 4 medio-basal setae.

Gonostylus narrowest near base, but with only little widening in either dorsal or lateral view; immediate basal region without setae, but dorso-lateral setae reaching far basally; 4-5 medio-distal setae in a continuous row with slightly weaker medio-basal setae; 1 subapical dorsal seta.

Types. Holotype: ♂ imago, Costa Rica, Osa, Rio Riyito, at light, January 1991, collector unknown, from coll. H. W. Riss, mounted in Euparal (ZSM). - Paratypes (Costa Rica, Rancho Quemado, collectors unknown, from coll. H. W. Riss): 3♂♂ imagines, September 1990; 2♂♂ imagines, November 1990; 1♂ imago, "Riyito", November 1990; 1♂ imago, "trampa II", December 1990, in Euparal (ZSM and in coll. M. Spies).

Distribution. *P. osa* so far has only been collected in light traps near several small streams of the Osa peninsula on the Costa Rican pacific coast.

Differential diagnosis. *Parachironomus osa* may be characterized by the absence of squamal setae, lack of caudo-lateral projections of the anal tergite, a straight gonostylus almost even in circumference throughout its length, and a slender anal point without distal widening.

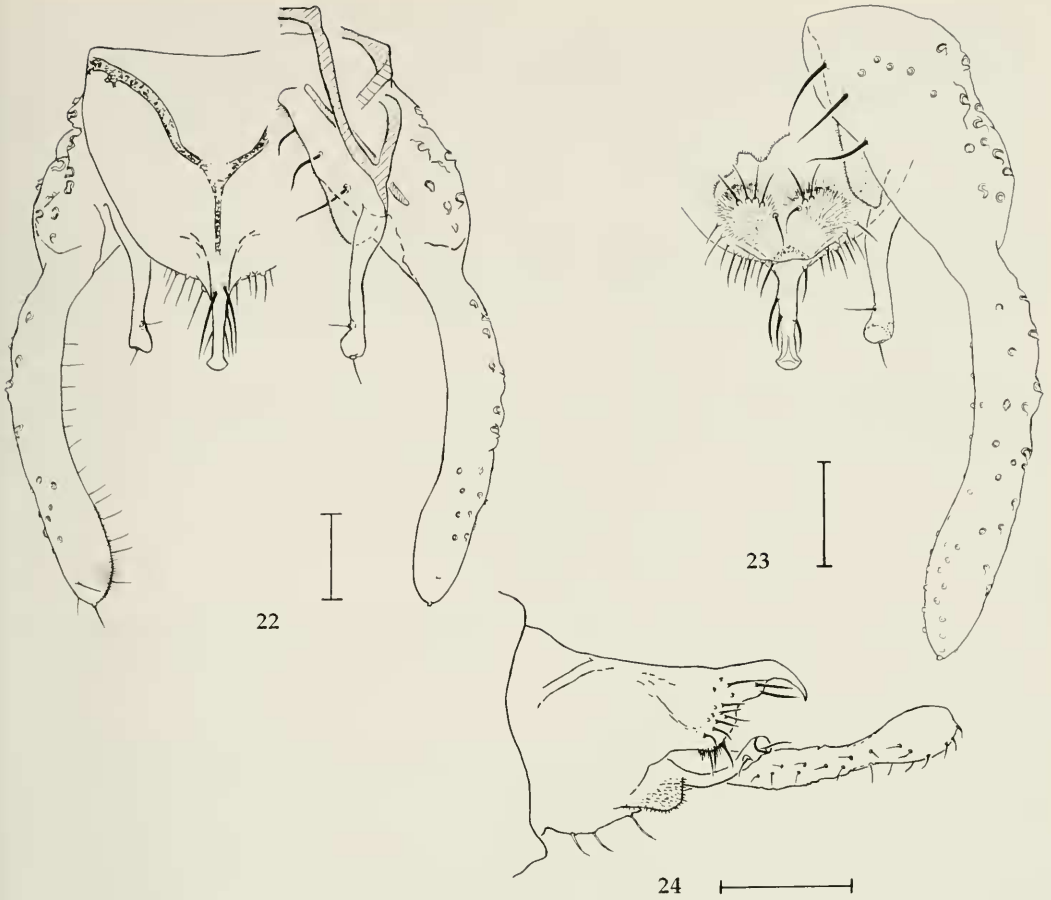
Parachironomus puberulus (Edwards), comb. nov.

Figs 22-25

Chironomus (Cryptochironomus) puberulus Edwards, 1931: 321

Imago ♂ (compare table 3)

The wing length of ca. 2.7 mm, given by Edwards (l.c.) for the dried and pinned holotype, was not nearly reached by any of the new specimens (1.70-2.21, M=1.99 mm; n=7).



Figs 22-24. *Parachironomus puberulus* (Edwards). Hypopygium. 22. Dorsal view. 23. Ventral view. 24. Lateral view. Scales: 50, 50, 100 µm.

Colour (after Edwards 1931). Thorax yellowish; vittae, postnotum (except at base), lateral ends of antepronotal lobes, median anepisterna II, preepisternum reddish brown to brown. Legs brownish, fore tibiae and -tarsi slightly darker. Abdomen olive, caudal margins of tergites 1-4 with narrow, dark brown lateral bands. Apices of gonostyli yellowish.

Head. Chilean specimen with 22 temporals, Bolivia (n=5): 12-17.

Wing. Argentina, Chile: membrane with numerous macrotrichia in all cells from r_{4+5} to an; veins (except Sc and M) also with macrotrichia, over almost their entire lengths; submarginal row on C extending to near arculus; 5-6 squamals. Bolivia: membrane macrotrichia only in cells r_{4+5} to m_{3+4}; veins Cu, Cu_1, and An without macrotrichia; submarginals on C not extending basally past RM; 6-12 squamals.

Legs. Lengths of segments in µm (left: Bolivia / right: Chile):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	745/700	620/500	975/900	530/500	405/375	305/280	135/110
P_2	685/680	660/610	390/350	240/210	165/145	105/ 90	70/ 65
P_3	825/780	870/810	690/610	340/345	300/275	170/155	90/ 80

Hypopygium (Figs 22-24). Anal tergite bands of Y-type, median connection often weak. Caudal region of anal tergite without lateral projections, but appearing indented dorso-laterally on each side of base of anal point. Anal point in dorsal aspect originating dorsal and anterior of anal tergite caudal margin, in lateral view (Fig. 24) with basal lobe; apical part slightly widened, curving to ventral. Anal tergite with ca. 15-20

Fig. 25. *Parachironomus puberulus* (Edwards). Distribution map.

(Argentina, Chile) or 30-35 setae (Bolivia): dorso-medially, around base of anal point, but mainly caudo-laterally; in ventral position (Fig. 23) a pair of circular cushions, densely covered with macrotrichia, and each bearing 3-5 setae pointing ventrally.

Superior volsella slender, curving from slightly median direction basally to dorsal and caudal; distal part slightly widened. Distal setal pit shallow (ARG, CHI; Fig. 22), or distinct (Fig. 24); median setal pit anterior of widened distal part of volsella.

Inferior volsella with bluntly rounded caudal projection, not reaching beyond margin of caudal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus narrowest at base, and slightly widened subapically; lateral contour rather evenly arched; dorso- to ventro-lateral surface rugose, and bearing numerous long to medium setae; 6-7 medio-distal setae, merging into almost equally strong medio-basal ones. 1 subapical dorsal seta in relatively lateral position; around the medio-distal stylus setae an area of up to 5 µm long macrotrichia.

Types. Holotype: ♂ imago, Argentina, Buenos Aires, San Isidro, 21/10/1926, leg. F. & M. Edwards. No other types designated. The hypopygium of the dried and pinned holotype has been separately mounted in Euparal, between two cover slips fastened to a cardboard carrier which was then stuck on the holotype pin (BMNH).

Further material examined: 2♂♂ imagines, Chile, Los Lagos, Rio Cruces at "Las Molinas" near Valdivia, in riparian vegetation, 11/11/1969, leg. F. Reiss; 11♂♂ imagines, Bolivia, side arm of reservoir between Oruro and Cochabamba, altitude ca. 3000 m, kinon, 14/7/1976, leg. E. J. Fittkau.

Distribution (Fig. 25) and ecology. The new records for *P. puberulus* raise more questions about the distributional limits of this species.

Edwards (l.c.) does not give the exact location, nor his collecting method, for the holotype. His "San Isidro" probably means a northern part of the city of Buenos Aires, situated on the Rio de la Plata. The

Chilean specimens were swept from riparian vegetation in a freshwater area influenced by tide induced water level fluctuations.

The Bolivian sample, taken from a reservoir at about 3000 m altitude in an area bare of vegetation, contained one ♂ imago of *P. supparilis* var. *longistilus*, which, like *puberulus*, has also been found in Buenos Aires province, Argentina.

Remarks

The Bolivian specimens - taken in surface drift, and appearing not fully hardened - differ from the southern records in several character details, most notably the depth of the distal setal pit on the superior volsella, and the extent of setation on the anal tergum and wing membranes. However, in light of the present knowledge these differences are not felt to warrant establishment of a separate taxonomic entity for the high Andean form.

Differential diagnosis. The occurrence of macrotrichia on cell membranes of the wing separates *puberulus* from all Neotropical *Parachironomus* but *vistosus*. In contrast to the latter, *puberulus* is lacking caudolateral lobes of the anal tergite, and pediform superior volsellae, but showing a unique ventral pair of pubescent pillows each bearing a group of ventrally oriented setae.

Parachironomus supparilis (Edwards), comb. nov.

Figs 26-32

Chironomus (Cryptochironomus) supparilis Edwards, 1931: 313
Parachironomus longistilus Paggi, 1977: 200. Syn. nov.

Note

P. supparilis is considered a superspecies in the sense of Mayr (e.g. 1975). Within its known morphological spectrum, four differing forms have been identified: *supparilis* sensu Edwards, *longistilus* after Paggi (1977), and the new variations *valdiviensis* and *centralis*. Table 2 compares these superspecies components'

Table 2. Character data for *Parachironomus supparilis* superspecies components.

character (♂ imago)	*supparilis* sensu Edwards	*valdiviensis* var. nov.	*longistilus* sensu Paggi *	*longistilus* Brazil	*centralis* var. nov.
wing length [mm]	2.30-2.88 (M=2.48; n=7)	1.85-2.08 (M=2.03; n=3)	1.6-2.5 (x=2.08; n=19)	1.27-1.50 (M=1.35; n=4)	1.25-1.88 (2)
temporals	18-21	10-15	12-19	12-22	–
frontal tubercles [µm]	∅ 3-5	∅ 3-4	LxW 10-23 x 10-15	LxW 10 x 6	–
AR	1.99-2.60 (M=2.24; n=8)	2.19-2.37 (M=2.24; n=3)	2.0-2.30 (n=6)	2.06-2.43 (M=2.24; n=6)	–
clypeus setae	14-15	17-21	14-22	16-17	18-20
palpomere lengths 2-5 [µm]	50,110,140,195	50,105,145,210	40,115,155,185	35,95,130,180	35,90,120,170
acrostichals	12-13	12-14	9-16	12-14	12-16
dorsocentrals	12-13	8-9	9-13	7-10	10
prealars	3-4	3-5	4	3-4	3-6
scutellars	9-10	12-13	12-16	8-10	6-12
FV	0.38-0.42 (8)	0.41-0.42 (2)	0.44	0.42-0.45 (4)	0.42-0.45 (2)
VR	1.18-1.31 (8)	1.23-1.35 (2)	1.14-1.18 (5)	1.14-1.22 (4)	1.15-1.19 (2)
squamals	9-21 some submarginal	5-7	5-15	4-6	3-6
LR_1	1.65-1.74 (M=1.66; n=6)	1.71-1.79 (2)	1.49-1.61 (M=1.58; n=3)	1.73-1.78 (M=1.75; n=4)	1.65
LR_2	0.49-0.52 (2)	0.52-0.53 (2)	0.49-0.54 (3)	0.53-0.59 (5)	0.57
LR_3	0.66-0.70 (3)	0.70-0.75 (2)	0.69-0.75 (3)	0.76-0.79 (3)	0.70
tibial spurs	rel. short to absent	normal	normal	normal	normal

* Data combined from Paggi (1977) and own observations (underlined)

observed characters outside of the hypopygium. To illustrate extensions to the *longistilus* ranges, the new Brazilian records are listed separately. Figures 26-31 give outlines of the key hypopygial structures.

The following description contains attributes not listed in tables 2 or 3, and repeats the most notable differences between the variant forms. For each character, statements refer to *supparilis* sensu stricto and all other superspecies components not separately mentioned.

Imago ♂

Colour. Head dark to blackish brown, incl. antennae and palpi. Thorax base colour brown; dorsal area between vittae (with the exception of a median, orally pointing triangle immediately anterior of scutellum), scutellum, oral margin of postnotum, median anepisterna II, preepisternum dark brown; vittae, margins of scutellum, postnotum (except at base) blackish brown. Legs brown, forelegs sometimes darker than others. Abdomen brown; caudal margins of tergites 1-4 darker; most dorso-median setal bases surrounded by areas of little pigmentation. *Valdiviensis, longistilus* (Argentina): similar pattern, but slightly lighter, abdomen (and sometimes thorax) with greenish tint. *Longistilus* (Brazil), *centralis*: base colour milky to golden brown, darkened pattern similar, but often faint.

Head. Frontal tubercles hemispherical. *Longistilus*: frontal tubercles about twice as long as wide. *Centralis*: unknown.

Wing. Some squamals originating from submarginal positions (*supparilis* only).

Legs. Lengths of leg segments in µm (left: *supparilis*, Chile, Laguna Diana; right: *centralis*, Brazil, Rio Solimões):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	870/580	690/445	1140/735	600/390	450/290	295/200	130/105
P_2	830/545	780/450	380/255	250/135	185/ 95	115/ 55	75/ 45
P_3	990/600	1060/620	695/435	410/230	345/210	180/ 80	85/ 65

Tibial spur length varying among localities (*supparilis* only), the largest spurs little longer than double comb height; specimens from Lago Futalaufquén (ARG) show no spurs at all.

Hypopygium (Figs 26-31). Anal tergite bands of Y-Type, median connection often weak; median longitudinal band reaches almost to base of anal point (*supparilis* only, others with bands of V- to broken Y-type). Caudal region of anal tergite without lateral projections. Anal point slender; base and apex in dorsal view slightly wider. In lateral view (Fig. 27) with basal lobe, slender, slightly curving to ventral. Anal tergite with field of ca. 15-20 setae dorsomedially, around base of anal point, and laterally.

Superior volsella (Figs 26, 27, 31e) - often abruptly - narrowing from base, pointing caudally without bending to dorsal; distal part little widened. 2 distinct setal pits; 1 usually spanning the width of the disto-dorsal area, the other in medio-ventral position. *Valdiviensis* (Fig. 31d), *longistilus* (Fig. 31c): Distal part distinctly enlarged, volsellae often appearing pediform with median projection, if so, dorsal setal pit decidedly narrower than width of projection. *Centralis* (Figs 31a,b): Distal part not widened, in lateral view appearing flat rather than globose. Dorsal setal pit comparatively shallow to indistinct.

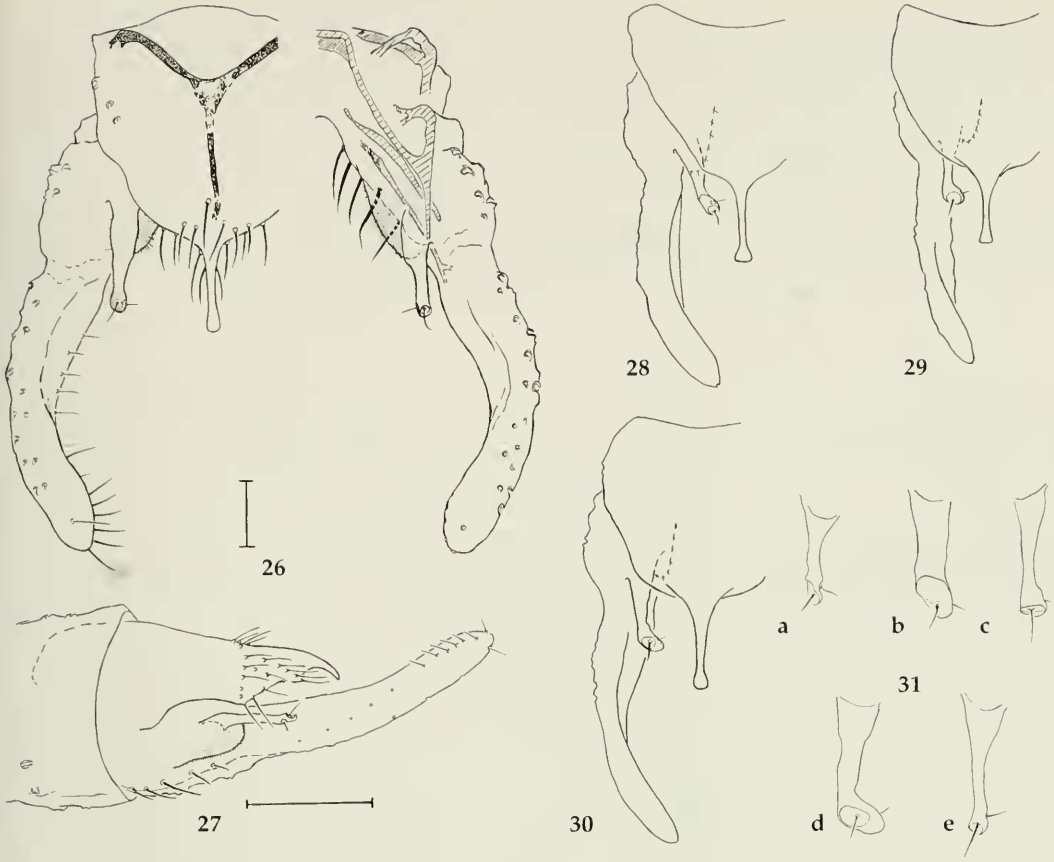
Inferior volsella with moderately pointed caudal projection, reaching at most slightly beyond caudal tergite. Gonocoxite with 3-5 medio-basal setae.

Gonostylus with basal constriction, relatively stout and straight proximal part, and narrower end curving to median and slightly dorsal. Apex bluntly rounded. Entire dorso- to ventro-lateral surface rugose and bearing numerous long to medium setae. 4-7 medio-distal setae. 1 subapical dorsal seta. *Valdiviensis* (Fig. 30): distal, curving part comparatively slender. *Longistilus* (Fig. 29): Gonostylus not curving to dorsal, and little to median, more uniform in circumference. *Centralis* (Fig. 28): Gonostylus lacking dorsal curving, basally wider than in *longistilus*.

Types. Holotype: ♂ imago, Argentina, Neuquén, Nahuel Huapi national park, Lago Correntoso, 18-25/11/1926, leg. F. W. Edwards. The hypoppygium of the dried and pinned holotype has been separately mounted in Euparal, between two cover slips fastened to a cardboard carrier which was then stuck on the holotype pin (BMNH).

The paratypes - 2♂♂ imagines, data see holotype; 1♂ imago, Argentina, Rio Negro, San Carlos de Bariloche, date unknown, leg. F.W. Edwards (BMNH) - have not been seen in this study.

Further material examined: *supparilis*: Argentina - 1♂ imago, Rio Negro, Lago Nahuel Huapi near San Carlos de Bariloche, in vegetation, 14/12/1969, leg. F. Reiss; 2♂♂ imagines, Chubut, Los Alerces national park, Lago



Figs 26-27. *Parachironomus supparilis* (Edwards) var. *supparilis*. Hypopygium. 26. Dorsal view, holotype. 27. Lateral view, Tierra del Fuego. Scales: 50, 100 µm.
Fig. 28. *Parachironomus supparilis* (Edwards) var. *centralis*, Rio Solimões. Hypopygium, dorsal view.
Fig. 29. *Parachironomus supparilis* (Edwards) var. *longistilus*, Belém area. Hypopygium, dorsal view.
Fig. 30. *Parachironomus supparilis* (Edwards) var. *valdiviensis*, Peulla. Hypopygium, dorsal view.
Fig. 31. *Parachironomus supparilis* (Edwards). Superior volsellae. a. var. *centralis*, Amazonas; b. var. *centralis*, Rio Grande do Sul; c. var. *longistilus*, Mato Grosso; d. var. *valdiviensis*, Valdivia; e. *supparilis* s. str., Chubut.

Futalaufquén, mouth of Arroyo H. Yrigoyén, 31/12/1985, in flight, leg. M. Spies; 1♂ imago, Tierra del Fuego, Rio Ewan (S), at "puente justicia" (bridge of national road no. 3), swarm, 18/1/1986, leg. M. Spies; 1♂ imago, 1♂ pupa, Tierra del Fuego, Tierra del Fuego national park, outlet of Lago Roca to Canal Beagle, swarm/ drift, 15/1/1986, leg. M. Spies; Chile, Ultima Esperanza - 1♂ imago, Laguna Diana, ca. 35 km E of Puerto Natales, in vegetation, 1/1/1971, leg. F. Reiss; 1♂ imago, outlet of Lago Balmaceda to Golfo A. Montt, ca. 26 km S Puerto Natales, in swarm of *Hilarempis* (Diptera, Empididae), 9/1/1986, leg. M. Spies. - *valdiviensis*: Chile, Los Lagos - 1♂ imago, Lago Todos los Santos, near hotel at Peulla, in flight, 2/12/1969, leg. F. Reiss; 5♂♂ imagines, Valdivia, pond on campus of Universidad Austral, "sample of imagines"/drift, 10/11/1969, leg. F. Reiss. - *longistilus*: holotype ♂ imago, Argentina, Buenos Aires province, district Chascomús, Arroyo Vitel, reared from benthos assoc. with *Ceratophyllum demersum*, 14/10/1975, leg. A.C. Paggi; 1 paratype ♂ imago, Arroyo San Felipe, other data see *longistilus* holotype; both permanent type mounts seen distributed over two microscope slides each, neither including the thorax. - Bolivia, 1♂ imago, side arm of reservoir between Oruro and Cochabamba, altitude ca. 3000 m, kinon, 14/7/1976, leg. E.J. Fittkau; Brazil (leg. E.J. Fittkau), Amazonas - 5♂♂ imagines, Rio Madeira at Paraná Madeirinha, at light, 11,12/9/1960; Pará - 3♂♂ imagines, Rio Cururu, at Missão do Cururu, at light, 12/1/1961; 10♂♂ imagines, Rio Tapajós, near Barra do São Manuel, at light, 13/1/1961; 1♂ imago, 2 pupal exuviae, 1 larva, Igarapé Cavallo, at Quatipuru, reared from submerged algae/grass, 7-9/4/1963; 1♂ imago, 2 pupal exuviae, Campo da Ponta Grande, near Quatipuru, reared, 8-11/4/1963. - *centralis*: Brazil (leg. E.J. Fittkau), Amazonas - 3♂♂ imag-

Fig. 32. *Parachirononus supparilis* (Edwards). Distribution map. A = var. *centralis*; B = var. *longistilus*; C = var. *valdiviensis*; D = *supparilis* s. str.

ines, lower Rio Solimões, "near home of P. Kraus", at light, 1/8/1961; 2♂♂ imagines, Rio Solimões, near Florianopolis, at light, 31/8/1961; Rio Grande do Sul - 1♂ imago, unnamed creek near Bom Jesus, altitude >1000 m, drift, 24-25/10/1961; 1♂ pupa, Paraguay, Laguna Escalante, Rio Pilcomayo, 31/3/74, leg. H. Sioli.

Distribution. Fig. 32 shows the locations, from which each of the superspecies components has been recorded so far. The *supparilis*- and *valdiviensis*-areas appear to be separated by the Andean divide, although the latter seems too low between Lago Todos los Santos and Lago Nahuel Huapi to preclude dispersal. While *centralis* and *longistilus* have not been taken together, their distributional relationship remains unclear. The single *longistilus* specimen from high Andean Bolivia was found in one sample with *P. puberulus*, which, like *longistilus*, has also been recorded from Buenos Aires province, Argentina.

Ecology. The one red thread running through the available collectors' field notes is the presence of aquatic or inundated riparian macrophytic vegetation. Beyond this, none of the *supparilis* variants appears to be narrowly limited to a certain type of environment. For example, *supparilis* sensu stricto has been collected near a variety of water bodies, from sea level to about 850 m altitude. The only associated pupa

was caught drifting in the roughly 100 m wide, multi-channel outlet of large Lago Roca, fed by runoff from the Cordillera Darwin on the southern edge of Tierra del Fuego's main island. The Laguna Diana is a midsized, shallow, brownwater lake surrounded by smaller ponds. Its shores are sandy, in wind-protected areas harbouring *Scirpus* stands. The south branch of Rio Ewan at the sampling site was 8-15 m wide, 30-150 cm deep, and carrying moderately flowing medium brown water (spec. cond. 162 μS_{20}). Aside from the dominant pebbly to stony substrate there also were stillwater zones with fine-grained bottom, and areas of inundated grass near the banks. The highest summer water temperature measured at *supparilis* sites was 16 °C, the lowest specific conductivity 23 μS_{20}.

In two cases males were observed swarming about 2 m above grassy meadows near open water. Collection dates progressively shift from late November through mid January, the further south the samples were taken.

Remarks

Paggi (l.c.) describes the larva and pupa of *longistilus*, along with both adult sexes. In the present study, at least one associable ♂ pupa could be found for each of the four superspecies components. From the Quatipuru area near Belém, Brazil, larvae could also be identified by rearing. Tentative associations may further be assumed (by presence of pupae and adults in the same sample, and absence of simultaneous congeneric species) for two larvae each of *supparilis* and *valdiviensis*.

The Quatipuru pupae and larvae did not differ from the *longistilus* descriptions in any character given by Paggi (l.c.). The same holds true for most *supparilis* pupae, but there are also otherwise identical specimens with a distinctly separated hook row on abdominal tergite II. The accompanying larvae exhibit 15 teeth in an entirely convex array - as opposed to Paggi's 13-toothed mentum with lateral concavities. The premandibles of those new larvae bear three apical teeth subequal in length (in *longistilus* the third is markedly shorter). Larvae collected with *valdiviensis* also showed the new form of premandibles, serrated first chaetulae laterales, and a third, deeply bifurcate branch on the mandibular seta interna. *valdiviensis* pupae are distinguished by the presence of acute, conical prealar tubercles, where all other pupae examined bear only low, rounded lobes (Paggi's pupae were not available for the present study, and she does not mention prealar tubercles in her description). The single available pupa of *centralis* is too badly damaged for detailed analysis.

The above findings support the taxonomic conclusions drawn from the adult material. However, the low numbers of specimens studied, combined with insufficient knowledge of intraspecific character variation for South American *Parachironomus* early stages, should be kept in mind.

Differential diagnosis. Members of the *Parachironomus supparilis* superspecies complex may be recognized by their typical gonostylus structure, a fairly straight base and distal bend to median, especially of the dorsomedian contour. The combination of eye extension diagonals with only 5 facets, conspicuous frontal tubercles, and the lack of wing membrane macrotrichia, is also distinguishing.

Parachironomus ticuna, spec. nov.

Fig. 33

Imago ♂ (compare table 3)

Colour (in alcohol). Base colour brownish olive; vittae and fore legs (from distal end of femora) darker.

Head. Temporals in 1 row. Frontal tubercles not discernible (head split into 2 parts). Palpi with comparatively long segments 3 and 4.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	750	520	990	505	410	305	115
P_2	570	520	345	170	105	55	45
P_3	710	730	540	280	240	140	70

Hypopygium (Fig. 33). Transversal anal tergite bands not meeting medially, longitudinal band absent. Caudal region of anal tergite with low lateral projections (but see below under "Remarks"). Anal point originating near caudal margin of anal tergite, very long and slender, with little distal widening. Anal

tergite with 26 setae, grouped mostly dorsomedially, and around base of anal point; tip of low basal lobe at about midpoint of stem of anal point.

Superior volsella slender, curving from base to straight caudal, with little distal widening; apical setal pits divided only by a thin lamella directed to medio-caudal, one setal pit in distal, the other in median position; rim of distal pit drawn out into proximo-lateral projection.

Inferior volsella with fairly acute caudal projection, reaching slightly beyond anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus narrowest in basal region, widening to dorso-median lobe just proximal of moderately pointed apex; basal region with 2-3 lateral setae; 4-5 medio-distal setae, subapical dorsal seta in comparatively medio-proximal position.

Types. Holotype: ♂ imago, Brazil, Amazonas, Rio Solimões, ca. 20 km above Igarapé Uarini, at light, 4/9/1961, leg. E. J. Fittkau, slide mounted in Euparal (to be deposited at INPA, Manaus, Brazil).

Remarks

The single specimen available has been mounted in somewhat over-macerated, and flattened condition. Hypopygial areas most affected by this (compare Fig. 33) are expected to be the caudal regions of the anal tergite at the sides of the base of the anal point, and the disto-dorsal lobe of the gonostylus.

Differential diagnosis. *Parachironomus ticuna* is characterized by the following combination of features: lateral diagonals of dorsomedian eye extension with 6 facets each, squama with setae, anal point about $^2/_3$ the length of gonostylus.

Parachironomus tirio, spec. nov.

Figs 2b-c, 34, 35

Imago ♂ (compare table 3)

Size. Very small; wing length 0.83-1.09 mm (M=0.90; n=15), for specimens parasitized by Nematodes (refer to "Remarks") 0.82-0.95 mm (M=0.91; n=7), for ♂ intersexes = 0.82-0.85 (2).

Colour (in alcohol). Mostly pale greyish olive; vittae, postnotum (except "T"-shaped antero-median region), posterior anepisternum, and preepisternum brown; joint area between femora and tibiae occasionally brownish.

Head. Minute frontal tubercles (max. ∅ ca. 1 µm) usually present, but appear to be lacking on a few specimens. Antennae as in Figs 2b-c. AR = 1.03-1.50 (M=1.29; n=17), for parasitized males (11 flagellomeres) AR = 1.04-1.23 (M=1.155; n=10), for ♂ intersexes (less than 11 flagellomeres) AR = 0.74-0.82 (2).

Wing. Costal submarginals usually not reaching near RM. FV = 0.40-0.44 (M=0.42; n=14); for parasitized specimens FV = 0.40-0.41 (n=5); for ♂ intersex = 0.37 (1). VR = 1.21-1.32 (M=1.25; n=14); parasitized individuals: VR = 1.20-1.34 (5); ♂ intersex VR = 1.12 (1).

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	540/390	325/220	680/560	375/265	275/195	195/135	85/65
P_2	480/375	410/295	220/165	115/ 75	80/ 50	40/ 30	25/25
P_3	540/430	530/390	375/250	190/115	165/105	95/ 50	55/30

LR_1 = 2.0-2.52 (M=2.34; n=11); for obviously parasitized specimens LR_1 = 2.24-2.47 (M=2.38, n=6); for intersex = 2.18 (1). LR_2 = 0.51-0.59 (M=0.55; n=19). LR_3 = 0.59-0.73 (M=0.645; n=16).

Hypopygium (Figs 34, 35). Anal tergite bands of Y-type, median connection weak, median longitudinal band reaching to base of anal point; Caudal region of anal tergite without lateral projections. Anal point originating from caudal margin of anal tergite; base not much wider than moderately widened distal part. Anal tergite without dorsomedian setae, each side with 2 setae laterally on base of anal point, and 2-3 in caudo-lateral to -ventral area, one of the latter usually pointing to ventral (Fig. 35), in dorsal view appearing ventro-proximally of caudal contour of anal tergite.

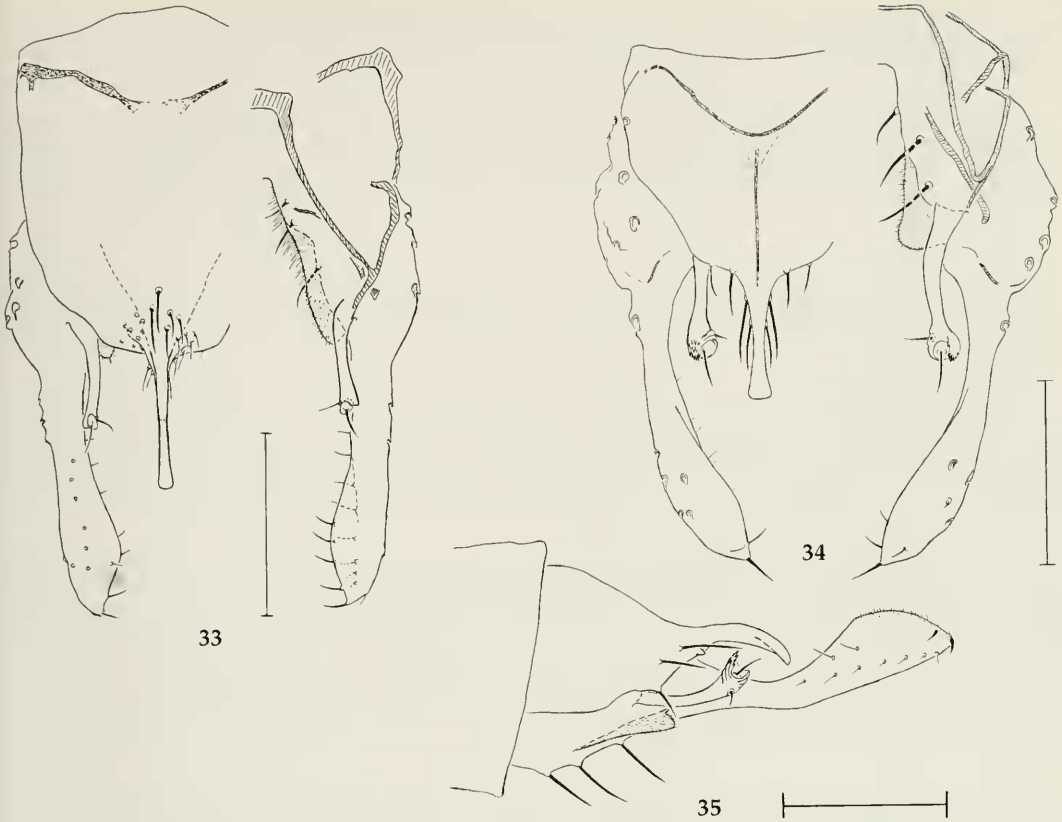


Fig. 33. *Parachironomus ticuna*. Hypopygium, dorsal view. Scale: 100 µm.
Figs 34-35. *Parachironomus tirio*. Hypopygium. 34. Dorsal view. 35. Lateral view. Scales: 50 µm.

Superior volsella slender, straight or slightly arched; distal part enlarged, bending to dorsal, often ringed with folds below deep disto-dorsal setal pit; outer proximo-lateral rim of distal pit drawn out into apically serrate projection bearing spicules on its proximal surface; median setal pit at base of distal part of volsella.

Inferior volsella with blunt to very low medio-caudal projection, not reaching beyond anal tergite. Gonocoxite with 3-4 medio-basal setae.

Gonostylus narrowest distal of base bearing 1-2 strong lateral setae; distal half of stylus curving to median, and slightly bent to dorsal, in lateral view (Fig. 35) widening to obliquely truncate end; 2-3 medio-distal setae, 1 subapical dorsal seta in lateral position.

Types. Holotype ♂ imago, Brazil, Amazonas, Rio Solimões, Mission Sta. Rita, 24/8/1961, at light, leg. E. J. Fittkau, slide mounted in Canada balsam (to be deposited at INPA, Manaus, Brazil).

Paratypes (Brazil, Amazonas, at light): 1♂ imago, Rio Marauiá, "ca. 20 km above mouth", 30/12/1962, leg. E. J. Fittkau; 1♂ imago, Rio Marauiá, "near equator", 2/1/1963, leg. E. J. Fittkau; 1♂ imago, Rio Negro, Ilha Marará, 8/2/1963, leg. E. J. Fittkau; 1♂ imago, Rio Cuieiras, above Igarapé Tukunaré, 19/12/1961, leg. E. J. Fittkau; 1♂ imago, Igarapé do Cachoeira, confluence Rio Cuieiras, 23/11/1962, leg. E. J. Fittkau; 2♂♂ imagines, Igarapé do Cachoeira, "Igapó near mouth", 26/11/1962, leg. E. J. Fittkau; 1♂ imago, Paraná da Terra Nova, ca. 2 km from mouth, 15/3/1961, leg. E. J. Fittkau; 1♂ imago, lower Rio Madeira, Paraná Madeirinha, 11/9/1960, leg. E. J. Fittkau; 2♂♂ imagines, port of Alenquer, 17/7/1946, leg. Sioli; 11♂♂ imagines, Rio Parú de Oeste, Mission Tiriyos, leg. E. J. Fittkau, 1962: 28/3/ (4♂♂), 29/3/ (1♂), 31/3/ (1♂), 3/4/ (2♂♂), 9/4/ (2♂♂), 21/4/ (1♂); 5♂♂ imagines (incl. 2 intersexes), Rio Cururú, Casa Lucio, 25/1/1961, leg. E. J. Fittkau, in Canada balsam (ZSM).

Further records: (Brazil, Amazonas, at light, leg. E. J. Fittkau): Rio Itu, 11/2/1962; Rio Cuieiras, ca. 50 km above mouth, 15/12/1960; Rio Cuieiras, confluence Rio Branqinho, 20/12/1961; Rio Negro, "opposite refinery

few km from Rio Solimões", 17/3/1961; Rio Parú de Oeste, "at Podostemonaceae site", 4/4/1962, Rio Parú de Oeste, Maloca Apicó, 20/4/1962; upper Igarapé Garapu, "at camp I", 24-27/8/1965; 1♂ pupa, Brazil, Amazonas, lower Rio Solimões, Lago Cabaliana at Manacapuru, drift, 6/7/1971, leg. F. Reiss.

Distribution and ecology. *Parachironomus tirio* has been collected near representatives of all Amazonian water types, throughout central Amazon lowlands, and in some peripheral regions. The only associated pupa was found in a black-water-influenced várzea lake on the lower Rio Solimões (see Reiss 1976).

Remarks

In 10 of 27 (37 %) individuals used for data collection on character states, 1 Nematode each was found to have parasitized the abdomen. In the Rio Parú population, afflicted specimens were 7 of 11 (64 %). 2 also parasitized individuals from the Rio Cururú sample stood out by possessing antennae with less than 11 flagellomeres (Fig. 2c).

Possible modifications of a variety of sexually dimorphous characters due to parasites have been documented for a number of Chironomid genera (e.g. Rempel 1940, Wülker 1961, Aagaard 1974). The frontal tubercles on the head of the imago have not been mentioned in this context. However, Paggi (1977), in her description of *Parachironomus longistilus*, lists the male's frontal tubercles as about twice the size of the female's. In *P. tirio*, parasitized specimens are among those with minute to indistinguishable frontal tubercles.

With the exception of the two collected antennal intersexes, character data for parasitized *P. tirio* are within the ranges of not obviously afflicted specimens. Wülker (1961) states, that "all" purely "antennal intersexes have male genital appendages", and regards their "intersexuality as extraordinarily low". On the other hand, according to the same author (l.c.), a certain amount of damage also alters the behaviour of the animals, to the extent that parasitized males are "rarely caught together with normal ones".

In the present study, no females of *P. tirio*, nor any larger sample of males clearly free of Nematodes could be examined. The possibility of parasitism influencing our character data should, therefore, be kept in mind.

Differential diagnosis. *Parachironomus tirio* is separate from all other known species of the genus in showing serrations and spicules on a distal projection of the superior volsella. The shape of the gonostylus, with its distinct bend to dorsomedian and somewhat truncate widening of the distal half, is also typical for this species.

Parachironomus vistosus Paggi

Fig. 36

Parachironomus vistosus Paggi, 1979: 47

In addition to Paggi's (1979) description, an examination of type material yielded the following noteworthy morphological details:

Imago ♂ (compare table 3)

Head. Frontal tubercles absent.

Wing. Consistent with all other specimens of *Parachironomus* seen in this study, no setae could be found on vein Sc.

Hypopygium. Anal tergite without dorsomedian setae, but with ca. 40 setae densely covering lateral protrusions of caudal region. In ventral position (Fig. 36), two pairs of setae situated on an apparent ledge posterior of the entrance to the inner genital area. Superior volsella with comparatively small and shallow distal setal pit; median pit distinctly anterior of enlarged, pediform distal part of volsella. Gonostylus with area of up to 5 µm long macrotrichia around the medio-distal setae.

A data table given by Paggi (l.c.: 53) to compare characters of *P. longistilus*, *vistosus*, and *robustus* unfortunately contains several erroneous entries. Contrary to the verbal description, *vistosus* is listed as possess-

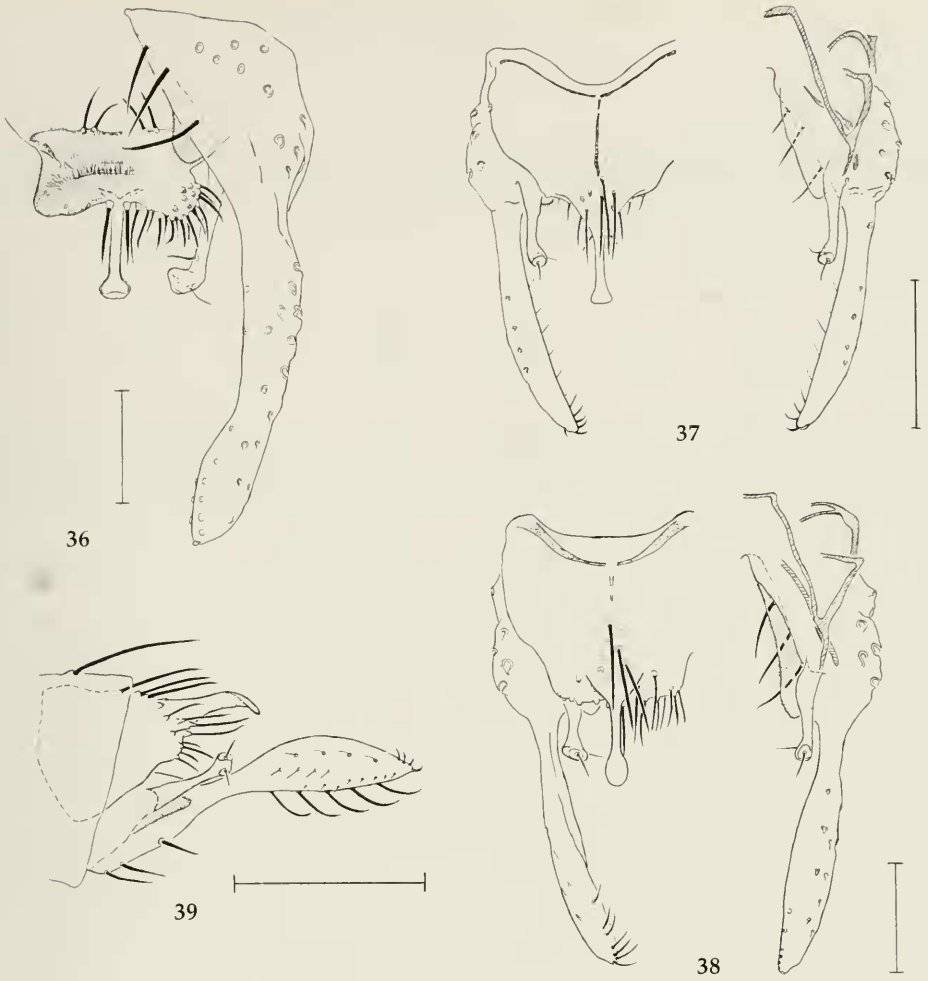


Fig. 36. *Parachironomus vistosus*. Hypopygium, ventral view. Scale: 50 µm.
Fig. 37. *Parachironomus waika*. Hypopygium, dorsal view. Scale: 100 µm.
Figs 38-39. *Parachironomus yanomani*. Hypopygium. 38. Dorsal view. 39. Lateral view. Scales: 50, 100 µm.

ing frontal tubercles, and lacking wing membrane macrotrichia. Furthermore, anal point lengths are given values little lower than those for the gonostyli.

Types (examined). Holotype: ♂ imago, Argentina, Buenos Aires province, Chascomús, adult sample, 7/3/1974, leg. A.C. Paggi (ILPLA: Instituto de Limnología, La Plata, Argentina). - Paratypes: 2♂♂ imagines, 1 with data same as holotype, the other from Arroyo San Felipe, 14/10/1975, otherwise same as holotype (ILPLA).

The permanently mounted parts of the holotype were found distributed over two microscope slides, 1 set of legs and the thorax were missing. The first paratype mount was missing head, 1 set of legs, thorax, and abdomen - the second paratype contained only the head without antennae, and the abdomen.

Distribution. *P. vistosus* so far is only known from the small type locality area in Argentina.

Differential diagnosis. From the only other Neotropical *Parachironomus* with macrotrichia on the wing membranes (*P. puberulus*), *vistosus* differs by the anal tergite bearing prominent caudo-lateral lobes, and two conspicuous pairs of ventro-median setae not arising from pubescent cushions.

Parachironomus waika, spec. nov.
Fig. 37

Imago ♂ (compare table 3)

Colour (in alcohol). Base colour yellowish brown, vittae reddish brown; antero-median vittal marks roundedly triangular, postero-lateral marks oval, all distinctly shorter than in any other *Parachironomus* seen.

Head. Third palpomere as long as fourth.

Thorax. Scutal tubercle not discernible due to damage.

Legs. Lengths of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	865	600	1100	575	490	410	155
P_2	735	640	400	200	115	75	45
P_3	820	840	580	290	240	140	75

Hypopygium (Fig. 37). Anal tergite bands of Y-type, longitudinal band reaching most proximal dorso-median seta. Caudal region of anal tergite with low lateral projections. Anal point originating near caudal margin of anal tergite; base almost as wide as the latter, extending to nearly mid length of anal point; distal part distinctly widened, sharply bending to ventral. Anal tergite with 15 setae: dorsomedially, around base of anal point, and laterally.

Superior volsella slightly sinuous, narrowing from base, and with moderately widening distal part; both distal setal pits conspicuous, median pit smaller, situated subapically.

Inferior volsella with broadly rounded (one body side) or moderately acute caudal projection, slightly extending beyond anal tergite. Gonocoxite with 3 medio-basal setae.

Gonostylus narrowest beyond base, very slightly curving to median, widest - but little widened - just caudal of mid length; basal region on one body side with one lateral seta, bare on the other; 4-5 medio-distal setae, subapical dorsal seta absent.

Types. Holotype: ♂ imago, Brazil, Amazonas, Rio Marauiá, Igarapé San Antonio, Cachoeira, at light, 8/1/1963, leg. E. J. Fittkau, slide mounted in Euparal (to be deposited at INPA, Manaus, Brazil).

Distribution and ecology. The type locality is situated in the drainage of Rio Marauiá - a northern tributary of the Rio Negro descending from the border mountains to Venezuela - just north of the equator, and at an altitude of about 100 m. Streams of the immediate vicinity are of predominantly white water type.

Remarks

The hypopygium of *P. waika* somewhat resembles that of the North American *P. carinatus* (Townes), especially as regards the superior volsella and gonostylus. However, in the only available *waika* specimen the caudo-lateral projections of the anal tergite are less pronounced, and the base of the anal point is much wider and longer than in *carinatus*.

The holotype and paratypes of *P. carinatus* could not be obtained for this study. Comparisons were made using 2 Florida specimens from the collection of Florida A&M University (courtesy of Dr. J. H. Epler).

Differential diagnosis. Among the species without prominent caudo-lateral projections of the anal tergite, *P. waika* may be identified by the broad, protruding base and marked distal widening of the anal point, and the lack of any of the special characters identifying fairly similar forms (flagellomeres and squamals: *aberrans*; ventro-caudal setae: *manaos*; short costal submarginal row: *osa*).

Parachironomus yanomani, spec. nov.
Figs 38, 39

Imago ♂ (Compare table 3)

Colour (in alcohol). Thorax base colour yellowish brown; vittae light brown; postnotum with 2 brown areas leaving lighter, antero-median "T"-pattern; abdomen and legs largely milky, occasionally areas around joints between femora and tibiae, and fore tarsi 1-3 brownish.

Head. 5 short, and 2 long temporals, all in a single row.

Legs. Length of segments in µm:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5
P_1	520/510	325/300	760/660	400/340	310/265	225/190	100/80
P_2	490/470	430/390	245/235	120/110	90/ 85	55/ 50	25/25
P_3	580/545	560/510	385/360	195/170	180/160	95/ 85	50/50

Tip of spur on longer comb of hind leg often bending outward.

Hypopygium (Figs 38, 39). Anal tergite bands not connected medially, longitudinal band weak to absent. Caudal region of anal tergite with lateral projections, but the latter - esp. in lateral view (Fig. 39) - not very prominent. Anal point in dorsal view originating anterior of caudal margin of anal tergite; base of anal point short, triangular; midsection slender; distal part in dorsal view ovally widened; anal point in lateral view (Fig. 39) without basal lobe, ventral contour with several shallow notches, meeting ventral side of distal widening near midpoint of the latter; anal point directed straight to caudal, only disto-dorsal widening part bent obliquely to ventral. Anal tergite with 6-9 comparatively long dorsomedian setae; 3 setae at or near each side of base of anal point; 3-6 setae on each caudo-lateral projection of anal tergite.

Superior volsella narrowing from base to stem, distal part little to moderately widened, with only little median projection; both setal pits distinct, the median one forming a medio-proximal excavation of distal part of volsella; lateral rim of disto-dorsal pit sometimes drawn out to a short projection.

Inferior volsella with moderately acute caudal projection, usually reaching slightly beyond anal tergite. 3 medio-basal gonocoxite setae.

Gonostylus in dorsal view narrowest near base, but, if mounted in ideal orientation, of almost equal width over entire length; in lateral view (Fig. 39) with midsection widening, and moderately pointed apex. Narrow base part of gonostylus without lateral setae; 5-7 medio-distal setae; 1 subapical seta in lateral position.

Types. Holotype: ♂ imago, Brazil, Amazonas, Rio Itu, at light, 10/2/1962, leg. E. J. Fittkau, slide mounted in Canada balsam (to be deposited at INPA, Manaus, Brazil). - Paratypes (Brazil, Amazonas, leg. E. J. Fittkau): 3♂♂ pupae, Rio Marauiá, "Seringeiro Tapiri above blackwater creek", drift, 2/1/1963; 1♂ hypopygium, Rio Marauiá, Mission San Antonio, at light, 21/1/1963; 1♂ imago, Rio Negro, "1h above confluence Rio Cuieiras", at light, 4/2/1963; 1♂ pupa, Rio Negro, "ca. 30 km below Barcelos", kinon; 1♂ imago and 2♂♂ hypopygia, lower Igarapé do Cachoeira, at light, 27/8/1965; 1 pupa, Rio Solimões, St. Luzia, kinon, 30/8/1961; 1♂ pupa, Paraná do Careiro, "5-6 km below beginning of Paraná", drift, 31/7/1961; 1♂ imago, Rio Madeira, Paraná Madeirinha, at light, 12/9/1960; 1♂ imago, upper Igarapé Garapu, ("camp I"), at light, 24-27/8/1965, in Canada balsam (ZSM).

Further record: Locus typicus, at light, 11/2/1962, leg. E. J. Fittkau.

Distribution and ecology. *P. yanomani* has mostly been collected in the central Amazonian lowlands, but also from the upper Rio Xingu area on the southern periphery. The habitat variety represented by the sample localities precludes any assumptions of specific ecological preferences or restrictions.

Differential diagnosis. *P. yanomani* is characterized by the following combination of features: Anal tergite with caudo-lateral projections and numerous dorsomedian setae, gonostylus straight, its midregion widened along dorso-ventral axis, distal part of superior volsella not ringed with folds.

Discussion

Of the 18 *Parachironomus* species now known from the Neotropics, 14 have been newly described here. With the exception of hypopygial structures and color patterns, Tab. 3 summarizes character data taken for all Neotropical species but *robustus* Paggi. The placement of *robustus* in *Parachironomus* is considered preliminary due to a high number of marked deviations from the genus norms as outlined above. The original description (Paggi 1979: 50) gives, among others, the following attributes: Dorsomedial eye extension of 3 facet rows. AR = 0.8 (n=2). 2 of the 9-10 dorsocentrals situated very far oral, separated from the others. R_{4+5} without setae. LR_1 = 1.20; LR_2 = 0.39; LR_3 = 0.55. Tibial spurs absent. Superior volsellae "short, stout, and with folds, apically excavated".

In Tab. 3 relationships within hypothetical species sets may be compared. The first two quarters of the table (pp. 92-93), for example, holds the Andean/Patagonian forms, and these five possessing squamal setae. The first and third quarters contain four species displaying somewhat truncate gonostyli (*ticuna* through *tirio*), and those with a high number of dorsomedian setae on tergite IX (*ticuna* through *atroari* except *tirio*). All cases of latero-ventral projections of the anal tergite are listed in the third and fourth quarters. The last quarter includes three species with fairly shallow setal pits in the superior volsellae.

The characters analyzed, however, offer few clues to the identification of phylogenetic boundaries between larger groups of species. Significant deviations usually occur in only one extraordinary case (13 flagellomeres: *aberrans*; elongate tibial spur: *atroari*; sparse wing vein setation, fused tibial combs with a single spur: *mirim*).

Zavrel (1933) was the first to notice that tropical species generally reach lower body sizes than those of temperate regions. The Neotropical *Parachironomus* examined also fit this pattern (see also Tab. 2). The

Table 3. Character data for Neotropical *Parachironomus* species. M = median; n = number of measurements; x = mean.

character (♂ imago)	*manaos*, spec. nov.	*osa*, spec. nov.	*ticuna*, spec. nov.	*guarani*, spec. nov.	*cayapo*, spec. nov.
wing length [mm]	1.35	1.11-1.20 (M=1.18; n=8)	1.57	1.12-1.47 (M=1.27; n=15)	1.07-1.45 (M=1.25; n=19)
temporals	12 in 2 rows	8-10 in 1 row	8 in 1 row	10-15 in 2 rows	11-14 in 2 rows
eye extension [facet rows]	6	6	6	6	6
frontal tubercles [µm]	–	absent to ∅ 2	–	LxW 5-7 x 3-5	LxW 3-6 x 5-8
flagellomeres	11	11	11	11	11
AR	2.06	1.52-1.59 (2)	2.2	1.73-2.31 (M=2.0; n=11)	1.50-2.03 (M=1.83; n=15)
clypeus setae	13	14-19	19	15-20	15-22
palpomere lengths 2-5 [µm]	30,85,120,180	25,85,105,160	30,120,160,220	30,85,115,175	30,100,130,185
acrostichals	13	7-11	12	10-16	10-13
dorsocentrals	7	4-6	12	6-7	6-10
prealars	3/4	3-4	4	3-4	3-5
scutellars	10 in 2 rows	6 in 2 rows	–	9-12 in 2 rows	10-19 in 2 rows
scutal tubercle	–	very low	–	distinct	low
wing macrotrichia	on C,R,R_1,R_{4+5}	on C (to R_1),R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}
FV	0.46	0.42-0.43 (3)	0.43	0.42-0.44 (4)	0.43-0.44 (2)
VR	1.13	1.22-1.25 (3)	1.21	1.16-1.25 (4)	1.19-1.22 (2)
squamals	absent	absent	4	absent	absent
LR_1	–	2.08-2.23 (2)	1.90	2.06-2.30 (M=2.20; n=11)	2.05-2.27 (M=2.13; n=9)
LR_2	0.57	0.61-0.64 (3)	0.66	0.63-0.65 (3)	0.57 (2)
LR_3	0.80	0.72	0.74	0.72-0.75 (3)	0.73-0.75 (2)
hind tibial combs	separate	separate	adjacent	separate	separate
tibial spurs	normal	normal	normal	normal	normal

larger tropical species - *waika* and *ticuna* - barely enter the lower end of temperate species size ranges. The largest specimen (*supparilis* from the southern tip of the continent) measured about 3.5 times the wing length of the smallest (*mirim* from Amazonia).

A good part of the character variation contained in Tab. 3 seems to parallel this overall gradient in body size. Included here are the numbers for temporals, clypeus setae, and the scutum setation. The antennal ratio also tends to be lower in the smaller species. The LR_1 exhibits an inverse trend, higher values associating with lower wing lengths. Regarding the AR and LR_1, again *waika* and *ticuna* bridge the gap between tropical and temperate value ranges.

Another set of characteristics shows little overall variation, or a distribution seemingly scattered across group limits. The ratios measured on the wing and mid to hind legs belong into the first category, palpomere lengths and the presence or absence of frontal tubercles into the second.

Rather than larger groups, three definite pairs of species can be identified using all available data: *P. puberulus* und *vistosus* are unique in bearing numerous macrotrichia on the wing membranes, anal points strongly hooked to ventral, and rather evenly curved gonostyli with comparatively long pubescence among the medio-distal setae. *P. guarani* and *cayapo* combine truncate gonostyli with slightly elongate frontal tubercles, and separate hind tibial combs. *P. matapi* and *apalai* feature comparatively wide anal points, superior volsellae with fairly shallow setal pits, and gonostyli whose distal regions form conspicuous median overlaps.

For 7 of the 17 species in Tab. 3 (*guarani, matapi, mirim, puberulus, supparilis, tirio, yanomani*), at least one male pupa could be associated. A cursory look at Amazonian pupal exuviae in collection at the Zoologische Staatssammlung revealed, that the diversity of forms belonging to *Parachironomus* is probably far greater than

Tab. 3. (continued).

character (♂ imago)	*puberulus* (Edw.)	*vistosus* Paggi	*aberrans* spec. nov.	*supparilis* (Edw.) *
wing length [mm]	1.70-ca.2.7 (8)	1.50-2.0 (x=1.81; n=7)	–	1.25-2.88
temporals	12-22 in 2 rows	14-15 in 2 rows	13 (+?) in 2 rows	10-21 in 2 rows
eye extension [facet rows]	5	5	6	5
frontal tubercles [µm]	absent	absent	∅ 6-7	LxW 4-23 x 10-15
flagellomeres	11	11	13	11
AR	1.67-2.03 (M=1.85; n=12)	1.66-2.03 (4) (x=1.83; n=5)	0.45-0.46 (2)	1.99-2.60
clypeus setae	11-20	21-26	18	14-22
palpomere lengths 2-5 [µm]	35,105,135,180	–	–	– *
acrostichals	11-18	10-14	18	9-16
dorsocentrals	8-13	8-13	9-10	7-13
prealars	3-4	4-5	4	3-6
scutellars	9-13 in 2 rows	10-13 in 2 rows	16 in 2 rows	6-16 in 2 rows
scutal tubercle	distinct	distinct	low	distinct
wing macrotrichia	r_{4+5} to m_{3+4} or an; C to M_{3+4} or An, not Sc,M	r_{4+5} to an; all veins except Sc,Cu,M	–	on C,R,R_1,R_{4+5}
FV	0.40-0.43 (8)	–	–	0.38-0.45
VR	1.18-1.21 (6)	1.12-1.16 (5)		1.14-1.35
squamals	5-12	5-7	2	3-21
LR_1	1.57-1.80 (M=1.67; n=5)	1.44/1.50	–	1.49-1.79
LR_2	0.56-0.59 (6)	0.53 (1)	–	0.49-0.59
LR_3	0.69-0.79 (4)	0.66/0.72	–	0.66-0.79
hind tibial combs	adjacent	adjacent	adjacent	adjacent
tibial spurs	normal	normal	–	absent to normal *

* Superspecies; see Tab. 2 for details.

the one presented here in the adult stages. The vast majority of the latter have been collected at lights, to which Chironomid imagines are relatively little attracted (Fittkau 1971). Consequently, with too little knowledge available on intraspecific variation, detailed descriptions of pupae were regarded as premature. However, comparisons were made to the preliminary species groups given for Holarctic pupae by Pinder & Reiss (1986). The 7 known Neotropical forms are split among 4 of the categories identified by Pinder & Reiss (l.c.).

P. supparilis, *matapi*, and *mirim* key to the *varus* group, combining 5 LS on each side of abdominal segment VIII with the lack of an anal comb. For a brief outline of *supparilis* pupae refer to the species description, section "Remarks". *P. matapi* stands out by the complete lack of pedes spurii A, and the presence of short and wide, apically blunt LS on segments I-III. 4 LS each on V through VII are grouped close together near the posterior end of each segment. The single specimen of *mirim* was not in sufficient condition for detailed study. It is interesting to note, that the pupa of the Nearctic *P. directus*, a species most likely very closely related to *aberrans*, also falls into the varus group.

P. puberulus and *yanomani* were taken to the *vitiosus* group. Segment VIII of the abdomen of *puberulus* bears 5 LS on each side, the posterior three of which are grouped around or between three small spicules of each anal comb. In several *yanomani* pupae a trend was observed, gradually reducing the posterior LS of segment VIII from the regular wide and long LS to a thin and short plain seta.

P. guarani pupae fit species group "B" of Pinder & Reiss (1986), with 4 LS on abdominal segments V through VIII, and a narrowly separated posterior hook row on tergite II. However, it should be noted that samples of exuviae of *supparilis* sensu stricto contained specimens both with and without median hook row gaps. Consequently, the separation of species groups ("B" and "C") based on hook row alone may not hold up.

P. tirio displays 1-5 relatively short spicules in the anal comb, and on sternite II two partially separated rows of long, slender spines pointing caudally. In the Holarctic *arcuatus* group, the spine rows are more

Tab. 3. (continued).

character (♂ imago)	*tirio* spec. nov. *	*waika* spec. nov.	*yanomani*, spec. nov.	*atroari* spec. nov.
wing length [mm]	0.83-1.09 * (M=0.90; n=15)	1.63	1.06-1.18 (M=1.11; n=4)	1.22-1.43 (M=1.35; n=6)
temporals	8-13 in 2 rows	9 in 1 row	7 in 1 row	9-12 in 2 rows
eye extension [facet rows]	6	6	6	6
frontal tubercles [µm]	absent to ∅ 1	absent	∅ 3-4	∅ 4-7
flagellomeres	11	11	11	11
AR	1.03-1.50 * (M=1.29; n=17)	2.41	1.63-1.79 (M=1.73; n=5)	1.69-1.92 (M=1.79; n=6)
clypeus setae	10-14	20	14-15	18-21
palpomere lengths 2-5 [µm]	30,80,125,180	30,125,125,210	25,75,110,160	25,75,120,185
acrostichals	8-14	17	10	10-16
dorsocentrals	4-7	10	4-5	7-9
prealars	3	5	3	3-4
scutellars	4 in 1 row	18 in 2 rows	6 in 1 row	11-13 in 2 rows
scutal tubercle	very low	–	low	very low
wing macrotrichia	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}
FV	0.40-0.44 (14)	0.45	0.43 (2)	0.42-0.43 (3)
VR	1.21-1.32 (14)	1.14	1.27-1.30 (2)	1.20-1.25 (3)
squamals	absent	absent	absent	absent
LR_1	2.0-2.52 * (M=2.34; n=11)	1.83	2.16-2.39 (M=2.27; n=4)	2.14-2.23 (M=2.18; n=4)
LR_2	0.51-0.59 (19)	0.63	0.57-0.60 (2)	0.55-0.60 (3)
LR_3	0.59-0.73 (16)	0.69	0.69-0.70 (2)	0.72-0.73 (3)
hind tibial combs	separate	separate	separate	adjacent
tibial spurs	normal	normal	normal	1 each very long

* Excludes obviously parasitized specimens; see species description and "Remarks".

extensively developed.

Pupae of *tirio* and *yanomani* are lacking pedes spurii B on abdominal segment II - said by Pinder & Reiss (l.c.) to always be present in Holarctic *Parachironomus*.

Cranston et al. (1989) state, that the present knowledge of the genus does not allow clear sets of imaginal characters to be associated with the established pupal groups. The Neotropical findings substantiate this judgement. Neither Tab. 3 data, nor hypopygial structures, would lead one to believe that, for example, *puberulus* and *yanomani*, or *supparilis* and *mirim*, are close to each other in a phylogenetic sense. The loss of anal comb spicules within the *Harnischia* complex is not limited to the *P. varus* group, and could have occurred in parallel in several groups of *Parachironomus*.

On the other hand, the variety of pupal characters within just a handful of species supports the notion gained from comparing the adults, that the known Neotropical *Parachironomus* fauna is systematically diverse, rather than easily split into larger groups.

Of the 18 South American species, 3 are limited to the Andean/Patagonian region, 11 essentially Amazonian, and 2 only found on the northern end of the continent. *P. supparilis* is found from Tierra del Fuego into central Amazonia, and *cayapo* from Brazil to Costa Rica.

As for many other animal groups, the separation of the South American Chironomid fauna into Guayanan/Brazilian and Andean/Patagonian subunits has been documented (Fittkau 1978). The phylogenetic relationship between these complexes is regarded as very distant. In the case of *Parachironomus*, however, for almost every attribute at first sight separating the species of different faunal subregions, there is a tropical exemption breaking the trend. *P. aberrans* and *ticuna* carry squamals and adjacent tibial combs (also present in *atroari*), *guarani* a distinct scutal tubercle. Only one character was found certain to identify the species occurring in the Andean/Patagonian subregion: the lower width of the dorsal eye extension. With ca. two

Tab. 3. (continued).

character (♂ imago)	*apalai*, spec. nov.	*matapi*, spec. nov.	*camajura*, spec. nov.	*mirim*, spec. nov. *
wing length [mm]	1.07	0.93-1.27 (M=1.15; n=11)	1.06-1.20 (M=1.17; n=5)	0.79-0.93 * (M=0.85; n=7)
temporals	9 (+?) in 2 rows	9-12 in 2 rows	8-12 in 2 rows	5-8 in 1 row
eye extension [facet rows]	6	6	6	6
frontal tubercles [µm]	absent	absent	absent	absent
flagellomeres	11	11	11	11
AR	1.53	1.62-1.75 (M=1.72; n=5)	1.79-1.87 (M=1.86; n=4)	1.03-1.25 * (M=1.12; n=7)
clypeus setae	18	14-18	17-21	11-13
palpomere lengths 2-5 [µm]	25,75,115,160	25,85,110,170	30,90,120,160	20,45,65,95
acrostichals	10	8	8	4-8
dorsocentrals	6	4-6	6	5-7
prealars	3	3	3-4	2, far apart
scutellars	4 in 1 row	5-6 in 1 row	8 in 1 row	2-4 in 1 row
scutal tubercle	very low	low	very low	low
wing macrotrichia	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}	on C,R,R_1,R_{4+5}	very few on R,R_{4+5}
FV	0.43	0.38-0.42 (4)	0.38-0.42 (3)	0.42-0.43 (2)
VR	1.20	1.20-1.27 (4)	1.16-1.27 (3)	1.21-1.25 (2)
squamals	absent	absent	absent	absent
LR_1	2.19	1.97-2.46 (M=2.32; n=6)	2.22-2.25 (2)	2.16-2.59 * (M=2.34; n=5)
LR_2	0.58	0.59-0.60 (4)	0.55-0.57 (2)	0.56-0.63 (7)
LR_3	0.71	0.63-0.71 (4)	0.65 (2)	0.67-0.77 (6)
hind tibial combs	separate	separate	separate	fused
tibial spurs	normal	normal	normal	hind legs: 1 each

* Excludes obviously parasitized specimens; see species description and "Remarks".

thirds of the world's *Parachironomus* fauna examined in this respect, lateral extension diagonals with 6 facets are only known from a few species outside of the South American tropics: the Nearctic *carinatus* (Townes) and *directus* (Dendy & Sublette), the Holarctic *frequens* (Johannsen), *digitalis* (Edwards) from Europe, and an undescribed form collected at Fitzroy River, Western Australia. All of the latter differ rather widely in hypopygial, and also pupal, characteristics. Considering further, that in the *supparilis* complex there is a design successful in both Neotropical faunal subregions, it seems that the gap between the latter for *Parachironomus* does not prove quite as wide as expected. An explanation for this fact could be found in the autecology - of *supparilis*, but probably also others - possibly tied more to habitat type and food source (submerged macrophytes), than to variable environmental conditions like water temperature and chemistry.

Adults and pupae now identified from the Neotropics extend the known character value limits for the genus *Parachironomus*. The antenna of *aberrans* represents the extreme in this respect. The value ranges for wing length and LR_1 are widened by including the South American species. The minimal wing length of 2 mm given for the Holarctis (Cranston et al. 1989), however, has been found to be too high by examining reference specimens in the collection of the Zoologische Staatssammlung. In spite of that, the smaller of the tropical new species still assume the lower end of the generic size scale. Probably directly connected to this (compare discussion of Tab. 3 data) is a simultaneous raise of the upper limit for LR_1 from values around 2 to 2.6.

Our reference collection further shows, that Holarctic *Parachironomus* tibial combs are not generally separate, as was stated in Cranston et al. (l.c.). Also, contrary to Lehmann (1970), European species do not always lack scutal tubercles. Both attributes probably show as varied development as they do in the Neotropis.

Macrotrichia in the wing membranes so far have been found in 3 Nearctic species - *chaetoalus* (Sublette), *hirtalatus* (Beck & Beck), and *potamogeti* (Townes) - as well as on the Andean/Patagonian *puberulus* and *vistosus*. The pupae of all North American representatives of this complex key to the *varus* group. The discovery of a different pupa for *puberulus*, along with the lack of hypopygial affinities between the two geographical species sets, precludes an explanation for the apparently disjunct, parallel occurrence of cell macrotrichia.

Wings completely bare of squamals are extremely rare in the global *Parachironomus* fauna outside of South America. Only *P. carinatus*, and *alatus* (Beck) from North America display this trait, *sublettei* (Beck) and *directus* each only 2-3 setae per squama. *alatus* is considered only tentatively placed in the genus by Beck & Beck (1969), and Saether (1977), due to superior volsellae lacking the typical setal pits but covered with microtrichia, as well as aberrant pupal characteristics. The others - like the Neotropical species bare of squamals - are among the smallest forms within their faunal region.

In the *Parachironomus* species examined, the superior volsella represents the most variable morphological attribute. Even between the two sides of an individual body, aspect differences are common, sometimes leading to the impression that the volsella's shape may be actively varied by its living bearer. With respect to the setae, and frequent other delicate distal structures, a sensory or stimulative function of the superior volsella during mating may be assumed. A lateral, beak-like, or rounded, apical projection - in European *Parachironomus* a very common feature, but much less often seen in the Nearctis - is present in a low expression with a few northern Neotropical species (*guarani*, *manaos*, *osa*, *ticuna*). The one notable exception is *P. tirio*. The same geographical pattern holds true for the relationship between the setal pits: whereas in a number of Holarctic forms these pits are equal in size, and located in opposite apical positions, most South American superior volsellae show at least a slight move to proximal, and reduction in size, of the median pit. *P. apalai* and *ticuna* most resemble the symmetrical form.

Caudo-lateral projections on the anal tergite are also considered parallel developments on different branches of the generic tree. For variations in adult and pupal characters among the Neotropical species in question see Tab. 3 and the discussion above. Such "shoulders" also occur in some of the Afrotropical members of *Parachironomus*, e.g. *coronatus* (Kieffer), *dewulfianus* (Goetghebuer). As in *vistosus*, these structures there appear more laterally than ventrally, and in a different shape. Furthermore, the African species exhibit at best only shallow setal pits on their superior volsellae. The most extreme tergite projections have been seen on the already mentioned undescribed specimen from Australia. They are acutely triangular, densely covered with setae, and point as much to lateral as to caudal.

The closest relatives to tropical South American *Parachironomus* - may be for want of knowledge about the Central American and Caribbean faunas - are found in two North American forms. For the relationship of *P. aberrans* to *directus* see the above description. The second case concerns *P. carinatus* (Townes 1945: 158), a species widely distributed in the Eastern USA, from New York State and Florida into the midwest. Apart from being the only Nearctic *Parachironomus* described without setae on the squama, and possessing

the tibial spur arrangement given in the Neotropical generic diagnosis, *carinatus* also displays the wide, "tropical" eye extension, and a caudal region of the anal tergite in dorsal view resembling lateral projections. Townes (l.c.) calls the gonostylus in lateral view "spatulate". The wing length (combined from several authors) ranges from 1.25 to 1.9 mm, AR = 1.9-2.2, LR_1 = 1.9-2.1. The pupa keys to the *vitiosus* group, and is lacking pedes spurii B (Beck & Beck 1969). These features indicate South American *P. yanomani*, or possibly *waika*, as its closest relative. In the Nearctis, *carinatus* appears to be systematically isolated. If from its wide distributional range one may deduce a relatively high ecological tolerance, then this species probably represents one of the rare examples (Fittkau 1978) for a successful leap from the Neotropical evolutionary center of a group into the North American continent.

In summary, biogeographic affinities of the Neotropical members of *Parachironomus* seem strongest to the Nearctic faunal region. Transantarctic relations as documented by Brundin (1966) can not be shown, due to a lack of knowledge especially of the Australian and New Zealand faunas. The only two species described from the Australis, *deliuificus* (Skuse) from Australia, and *cylindricus* (Freeman) from New Zealand, are regarded only tentatively placed in the genus (Saether 1977).

The material collected in greater Amazonia is by far not yet worked up quantitatively. As has been indicated in the discussion of pupal exuviae, estimating the total number of tropical *Parachironomus* species at 50 -100 percent higher than the one now described does not seem exaggerated. This even excludes several already known forms possessing superior volsellae with distal setae arising from distinct pits, but also bearing more or less extensive patches of microtrichia on these volsellae.

For these reasons, the outline given here for the morphological spectrum of South American *Parachironomus* should by all means be regarded preliminary.

Acknowledgements

Collections from the Amazon region were taken in collaboration of the Max Planck Institute for Limnology in Plön, Germany, with the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil. Finding *Parachironomus* in Tierra del Fuego became possible thanks to Dr. Thomas and Renate Gonser, Kastanienbaum. Costa Rican specimens were kindly made available by H. Wolfgang Riss, Zürich.

For loans of specimens we are indebted to the following colleagues and institutions: Dra. Analía C. Paggi, Instituto de Limnología La Plata, Argentina; Dr. John H. Epler, Crawfordville, Florida A & M University, Tallahassee; British Museum (Natural History), London; U.S. National Museum of Natural History, Washington, D.C.

A part of this work is based on a thesis completed by the first author in partial fulfilment of the requirements for the Diploma in Biology from Ludwig-Maximilians-Universität, München, Germany.

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